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E.W. Sexton

OBITUARY

MRS E. W. SEXTON, F.L.S. (1868–1959)

Mrs Alice Wilkins Sexton (*née* Wing) was born at Truro on 27 April 1868 and brought up by parents who, as she related, regarded natural science as no fit subject for a young lady, nor believed it proper for young ladies to study at colleges. Her later life revealed itself as a splendid reaction to this upbringing.

During her childhood some periods were spent in Banffshire and Galway, but a permanent change of surroundings occurred in 1885 when the family moved from Truro to Plymouth. Here she later married Mr L. E. Sexton, a dental surgeon with scientific interests, a keen supporter of the Plymouth Athenaeum, and a friend of the late Dr E. J. Allen. In 1900 Mr Sexton became a member of the Marine Biological Association. An outlet was now provided for his wife's interest in animals and exceptional talent for drawing and painting. As can be seen from her oldest surviving sketches, it is in this year that Mrs Sexton's work in the field of marine biology properly began.

Polychaete worms and Crustacea provided her main subject matter. The first illustrations to be published (in 1902) were twelve plates in T. V. Hodgson's report on the Crustacea of the 'Southern Cross' expedition. She then illustrated certain polychaetes for two of Dr Allen's papers published in 1904.[1] Further drawings of crustaceans and pycnogonids illustrated articles by L. H. Gough,[2] T. V. Hodgson,[3] and R. Gurney.[4] All these appeared under the signature of 'E. W. Sexton', from the circumstance that the name 'Elsie' had been adopted in place of Alice, and this name was never after to be discarded.

These earlier drawings showed an unusual ability for depicting detail accurately, a feature that was to be so conspicuous in her later work. Examination of the plates in Hodgson's 'Southern Cross' Report gives no clue that these were in fact reproduced without any reduction.

It is not surprising, then, that Prof. McIntosh accepted some of her illustrations of syllids for the current volume of his polychaete monograph (Vol II, No. 1), notwithstanding the very high standard set by Miss A. Watson, his regular artist. Some coloured illustrations of the syllid *Procerastea*, included in three plates of Allen's paper[5] published in the *Phil. Trans.* much later on, in 1921, can only be described as wonderful. Many, however, of her drawings and paintings of polychaetes have never been published: they survive in two albums (one started in 1901, and the other, the larger, in 1909).

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[1] *J.M.B.A.*, Vol. 7, p. 299 and *Q.J.M.S.*, Vol. 48, p. 79 (1904).

[2] Report on the plankton of the English Channel in 1903.

[3] *Ann. Mag. nat. Hist.* (7), Vol. 14, p. 458, and *National Antarctic Exped.* 1901–4, Vol. 3.

[4] *Spolia Zeylanica*, Vol. 4, p. 126.

[5] *Phil. Trans.* B, Vol. 211, p. 131 (1921).

But Mrs Sexton was not destined to remain simply an illustrator. In August 1906 Dr Allen went on a 5-day cruise in the S.S. 'Huxley' to the northern part of the Bay of Biscay and brought back a collection of invertebrates. He offered the Amphipoda to Mrs Sexton to examine. This task she set about with vigour and thoroughness. By the time she had dealt with the thirty-five species represented she had made contact with the leading specialists of the day, obtained loans of type material from several Museums, and had gone far in becoming a specialist herself in the study of Amphipoda. This group was, in fact, to provide the chief subject of her work for the rest of her life. Her first publications appeared in the *Proceedings of the Zoological Society* of 1908 and 1909, two first-rate taxonomic papers.[1] To a reader of these to-day it is difficult to realize that the author had had no academic zoological training.

While continuing taxonomic studies—collections from Hamburg and Königsberg Museums were next examined—Mrs Sexton now embarked on a plan to study in detail the life-history of a species that could easily be reared in the laboratory. Among Amphipoda almost nothing was then known of the number of stages passed in reaching maturity, or of the degree of change between one stage and the next. *Jassa* was first chosen, but after considerable effort the difficulty of breeding it proved too great. Its study, though renewed later, was eventually abandoned, not altogether without results of interest.[2] Attention was then turned to *Gammarus*.

It happened that both the German collections were mainly from brackish and fresh water, and contained various samples of an unnamed *Gammarus* previously confused either with *G. locusta* or with *G. duebeni*. Though particularly struck by the fact that the animals from the more saline localities were less hairy than those from fresher water, Mrs Sexton assigned them all to a single variable species, which she described as *G. zaddachi*. Various localities were then examined near Plymouth for *Gammarus*, and overlooked species were discovered (though, curiously, *zaddachi* itself remained unobserved until it was pointed out by a visitor from Australia twenty years later). Notably, a collection from the brackish ditches of Chelson Meadow, made on 4 June 1912, produced in abundance a distinct species of smallish size, to be described by Mrs Sexton as *G. chevreuxi*. For many years Chelson Meadow was its only known habitat. Two pairs of the original collection were set aside for detailed observation and for providing broods for experimental rearing in different salinities. Mrs A. Matthews assisted in this research, which was carried out in the Plymouth Laboratory: up to now Mrs Sexton

[1] *P.Z.S.* (1908): p. 370; (1909): p. 848.

[2] Sexton & Reid (1951), *J. Linn. Soc.*, Vol. 42, p. 29.

had apparently worked in her own home in Higher Compton under Dr Allen's remote control.

The results were unexpectedly fruitful, for they led to an entirely unforeseen line of research. For it was from the progeny of one of these pairs that the first mendelian recessive type was bred out—an animal with red, instead of black, eyes. Other variations affecting the eye pigments were soon observed, some behaving in a simple mendelian manner, others not. These were still relatively early days in the study of the new genetics, and hardly any invertebrates other than insects had been studied for mendelian inheritance. The outcome of the extensive breeding work then undertaken with the collaboration of Dr Allen was looked upon with more than ordinary interest, and *G. chevreuxi* began to attract attention as a useful experimental animal.

The occurrence of intersexes in one of the laboratory strains provided the occasion, in 1920, for collaboration with a rising young zoologist, J. S. Huxley, in an attempt to trace the cause of this phenomenon. While genetic work continued, the original aim of making a detailed study of the life-history of *G. chevreuxi* was eventually achieved in 1924. The successive stages of both male and female are illustrated in detail, based on the examination of successive moults of numerous individuals, and the result is a classic of its kind.

In the mean time the genetic work had received a new stimulus with the appearance of more red-eye recessive types in collections made in 1922, and another recessive concerned with the lack of body pigment. An additional incentive about this time was the belief that the 'mutant' types may have originated under the influence of heat or other abnormal conditions. As work continued through the years into the 1930's it was appreciated by degrees that the wild population carried a high proportion of recessive genes which were exposed in the laboratory by in-breeding. This in itself is a fact of much interest, its cause and significance being still imperfectly understood.

One of the mutant strains was kept going for many years in the Oxford Zoological Laboratory, where E. B. Ford used it successfully, not only in practical genetic classes but also experimentally in illustrating the essentially dynamic action of genes. Mrs Sexton had always appreciated the opportunities that *Gammarus* afforded for tracing the development of any given character during successive growth stages, a possibility not afforded by holometabolous insects like *Drosophila*.

Not long after the death of her husband Mrs Sexton was appointed to the Laboratory staff, on 1 April 1924, as the Director's Research Assistant, a post she held until 1948 when she officially retired. She had just completed a guide to the Plymouth aquarium, which L. R. Brightwell illustrated.

During the years that followed, the work involved in maintaining the diverse 'mutant' stocks of *Gammarus chevreuxi* became particularly arduous. The variety of eye-colour types had multiplied and required careful assessment.

A continuous succession of broods had to be sorted, their characters noted, and periodically re-examined; pairs had to be intelligently mated, and dead animals preserved; then histories had to be catalogued, and the final results charted. This task she fulfilled with never more than one part-time assistant—her sister Miss M. B. Wing at the beginning and then, for at least 20 years, Miss A. R. Clark.[3] The genetic work on *G. chevreuxi* was not wound up until 1936.

After this Mrs Sexton turned to accumulated arrears of *Gammarus* taxonomics, describing *G. tigrinus* from the Midlands, giving a revised account of *Marinogammarus* species (in collaboration with G. M. Spooner), and writing a fuller description of *Gammarus zaddachi*. Finally she produced a very complete review of *Jassa falcata*, including results of her earlier unpublished work, a task in which she was helped by the late D. M. Reid. She passed her 80th birthday before the latter work was completed, yet her ability to produce accurate illustrations showed no sign of deterioration. It was her failing eyesight that eventually called a halt to her remarkably sustained scientific activity. In 1957, after the death of her only daughter Mary in 1951, she left Plymouth to spend her remaining years with her son, Col. F. B. W. Sexton, in Sussex. She died on 18 February 1959 in her 91st year.

Mrs Sexton had great vitality, determination, and independence of outlook. Those who, on rare occasions, offered direct or implied criticism of her work were summarily treated, student[1] and professor[2] alike. She held firmly to any belief she had once formed.

Her great contribution was the excellence of her illustrations and descriptions. There is rarely any doubt what she is describing, and later specialists can rely on her data for forming their own interpretations. In drawing amphipods and their parts she is superior even to G. O. Sars, for paying that much more critical attention to detail. Her technique, moreover, had to be accommodated to the requirements of the line-block and dispense with shading effects, a limitation Sars never had to contend with.

Those who were privileged to know her found in her a generous and sympathetic friend. Visitors to her home at Reservoir House (to which she moved after her husband's death) were received with the kindest hospitality. Her garden was full of botanical treasures from all over the world, and these she exhibited with delight. She had special regard for young biologists whom she was always eager to help. For children also she had a particular fondness, and the photograph here reproduced shows a characteristic aspect. With her, holding a child, is her daughter Mary (Miss M. A. F. Sexton) who was Librarian at the Plymouth Laboratory when she died in 1951. G.M.S.

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[1] *Nature, Lond.*, Vol. 136, p. 477.

[2] *J.M.B.A.*, Vol. 21, p. 407.

[3] *J.M.B.A.*, Vol. 40, p. 459.

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THE RESPONSES AND ORIENTATION OF THE BIVALVE *LASAEA RUBRA* MONTAGU

By J. E. Morton
Department of Zoology, Queen Mary College, University of London

(Text-figs. 1–7)

Lasaea rubra, like other small Erycinacea, is unusual among eulamellibranchs in its relatively great mobility on the surface of the substrate. It can crawl about as freely as a small gastropod and lays down a mucous trail for the attachment of its progressing foot, drawing the shell and body rhythmically forward after each advance thrust of the foot. Unlike some other Erycinacea, *L. rubra* has no well-defined sole; it attaches by the sharp lower edge and part of the side of the foot, which is strongly ciliated and well supplied with mucous glands. In most burrowing eulamellibranchs, the site of communication with the surrounding water has shifted to the paired siphons at the posterior end. The Erycinacea, however, have an anterior inhalant siphon; and—as in forward moving prosobranch gastropods (Morton, 1958)—there is an obvious adaptive advantage in receiving the ingoing current from the water into which the animal is moving.

L. rubra lives normally attached by temporary byssus threads, nestling in small crevices between slate laminae, in irregularities of the rock surface, and especially in *Pygmaea* lichen tufts and inside the empty shells of the barnacle *Chthamalus stellatus* (Morton, Boney & Corner, 1957). It shows a marked thigmotaxis or preference for lateral contact. When removed from its site it appears at once very restless. Placed in a glass bowl in room light it shows three very obvious responses: it will crawl away from a source of light, it will take any opportunity to climb a sloping or vertical surface, and if enough specimens are close together they will ultimately aggregate in small clusters and attach to each other by byssus threads.

Lamellibranchs without eyes or exploratory tentacles are not usually thought of as direction-finding animals, and there appears to be as yet no account of migration by an adult eulamellibranch in response to external stimuli. This paper will present the results of some experiments to elucidate the responses of *Lasaea rubra* to the stimuli of light, gravity and lateral contact, and will attempt to show the relevance of these to its orientation and maintenance of position on the shore.

Material was obtained in the *Chthamalus stellatus* zone of the upper inter-area tidal at Tinside, Plymouth, being brought to the Laboratory in chips of rock or barnacle shells, and kept cool in the dark until used for experiments within, at the most, 2 or 3 h of collecting. The shell being closed when out of water, the animals received no immediately previous light stimulus, and were left attached *in situ* until a few minutes before the experiment. They were then immersed in watch-glasses of sea water only for so long as was necessary to moisten the shell and allow the very rapid emergence of the foot and siphon.

All experiments were performed in a dark box, a metre each dimension, with non-reflecting blackened sides. This was closed in front by a black curtain and kept in a dark room at a cool room temperature of 15° C. The experimental substratum was a glass sheet of 13 cm square, marked out with a working field 11 cm square, gridded with centimetre squares (Fig. 1 B). The animals crawled readily on this glass, providing a record of their own trails by the secreted mucous track. After an experiment such trails could be made easily visible by gently agitating the glass sheet in a suspension of talcum powder in water, and could then be dried and varnished; in practice it was found much more convenient and equally accurate to redraw them at once at the same scale on squared graph paper.

The apparatus for light-response experiments is shown in Fig. 1 A. It consisted of a galvanized iron photographic dish (*t*) 5 cm deep painted with black marine varnish and lined with non-reflecting black 'Cobex' plastic sheeting, with vertical sides and a 2 cm. margin turned inwards horizontally at the top to absorb small amounts of light reflected from the glass. The lamp-box (*b*) held a 12 V tungsten filament lamp with a luminous intensity in the direction of the experimental plate of 9·2 candelas. The colour temperature of the lamp was 2900° K. The filament (*l*) was 8 cm behind the aperture of the box. *p*–*p* 1 represents the glass plate on the floor of the dish, and *s* the beginning of the experimental field, 7 cm inside the lighted area. *s*–*s* 1 is the length of the light gradient used in the experiments. Illumination fell off laterally along the transverse line of *s* by 1 % at 2 cm from the centre of the light path, and by 4 % at the extreme edge of the experimental field. For the conditions of the experiment, and with the steepness of the *s*–*s* 1 gradient, transverse illumination at a given level was considered as being approximately uniform. Refraction and reflexion of light at the water surface were calculated as for an average angle of incidence of 20°; and the intensity of light incident at *s*–*s* 1 was taken to be approximately 40 % of the corresponding value at the water surface. The animal having no apparatus for light concentration or image formation, the illumination *I*, received at *s*, at a distance of 20 cm from the light source may be calculated

$$I = \frac{c}{(ls)^2} \times 0{\cdot}4 = \frac{9{\cdot}2}{0{\cdot}2^2} \times 0{\cdot}4 = 9{\cdot}2 \text{ lux},$$

where *c* is the luminous intensity of the source in candelas and *ls* the distance from the source in metres. Illumination at the far edge of the experimental field, *s* 1 30 cm from the source, will be 4·1 lux.

A series of neutral filters of optical densities 0·1–4·8 were in separate experiments placed in the light path at the aperture of the lamp-box at *f*. The greatest care was taken to avoid leakage of light around the filters.

For experiments involving gravity a rectangular glass trough was used, 20 cm deep, and the experimental glass plate was raised to the angle of inclination required by varying the length of a suspending wire. In experiments at a high angle of slope animals were given 3–5 min to attach by the foot to the glass plate, while at a lower slope; after this the plate was raised, any progress already made by the animals being noted and the resultant length of trail disregarded.

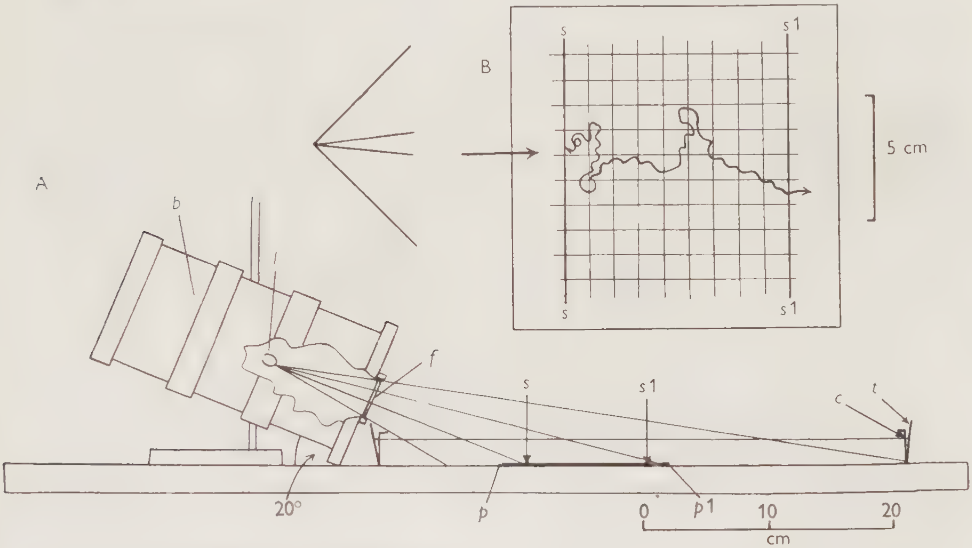

Fig. 1. A. (*a*) Apparatus used in experiments on photo-orientation; (*b*) lamp-box; (*c*) 'Cobex' dull surface lining sheet; (*f*) filter; *l*, light source of lamp; *p–p*1, experimental glass plate; *s–s*1, limits of experimental field; *t*, experimental trough. B. Experimental glass sheet showing the course of a trail, running across the gridded area. The arrow shows the direction of the light gradient falling off from *s* to *s*1, and approximately uniform transversely. Also shown are the angles +45 to −45, and +5 to −5 used in the presentation of data.

MOVEMENTS

The method of locomotion is illustrated in Fig. 2. The foot forms a slender tongue, perfectly colourless and translucent, that can be thrust out a distance equal to the length of the shell. From the anterior end, above the foot, also emerges the inhalant siphon, a short stout tube, somewhat laterally compressed; its margin is plain or sometimes very slightly crenate, and the opening can be narrowed by the margin drawing in. The tip of the fully extended foot is slightly flattened against the substrate and narrowly spatulate; but this is the only suggestion of a 'sole' and when lifted free the whole lower margin of the foot is sharp-edged and very narrow. A forward 'step' takes place in several stages (Figs. 2 B–E). From the resting position with the shell lying on one side or the other, the foot is put out and freely moved about, being thrust from side to side and curved beneath the shell as its pointed tip appears to feel for purchase. It attaches to the ground by the keel-like ventral edge and the lower part of one side, which is almost opaque and possesses mucous glands and cilia (see Popham, 1940). As it becomes fully extended the main site of attachment seems to be the sharp ventral edge. With the foot so extended the heavy shell is drawn forward upon it and hauled into an upright position, ventral margin lowermost, as the retractor muscles of the foot contract, first on the side remote from the ground as the shell is raised up, and then on both sides as it is drawn sharply forward. On completion of each step the foot is very short, with an angled 'heel' behind and projects in front little more than the length of the siphon. The foot is almost immediately extended again for the next step and the shell slumps to one side or the other, being raised vertically once more at the ensuing foot contraction.

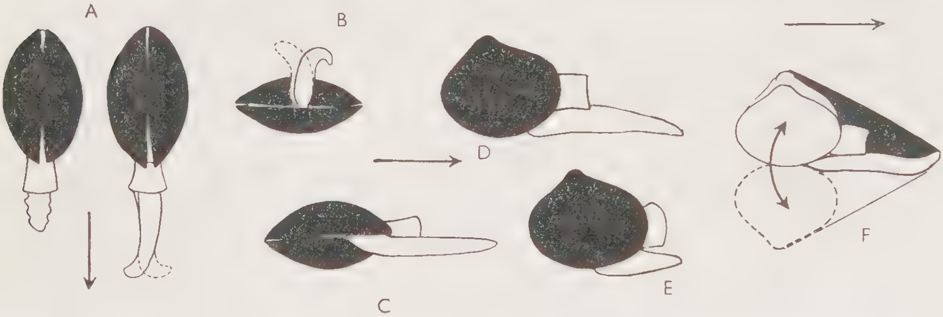

Fig. 2. *Lasaea rubra* showing the positions of the shell, foot and inhalant siphon at various stages of exploration and locomotion. A. Animal from above showing the retraction of the foot under strong light stimulus, and the action of the tip at its furthest extension. B–E. Four positions in a single forward 'step'. F. Illustration of the effect of the shell in shading the foot from illumination from behind, on either side alternately. The arrows show the direction of incident light.

Lasaea rubra has no macroscopically differentiated light receptors, but either of the two parts of the body (foot or siphon) exposed in front could—it was suspected—be responsible for the light sense and for detecting bilateral differences in light intensity at successive points of time—that is, to serve as receptors suitable for the type of reaction called a 'klinotaxis' by Fraenkel & Gunn (1940). In *Mya* and *Cardium* the posterior siphon tips, being alone exposed at the surface, are photosensitive and bear rudimentary 'eyes'. In Pectinidae the whole mantle margin bears tentacles and eyes forming the sensory outstations of the body. In *Lasaea rubra* the siphon is short and relatively immobile. Though it is probably diffusely photosensitive, the main exploratory role has passed to the tip of the foot, the anteriormost point of the body, which can, moreover, be freely moved about. During extension its tip can be slightly raised and curved tentatively to one side, then—after a momentary contraction—to the other. Rather more frequently after a movement to one side, the foot is partly or wholly withdrawn into the shell before emerging to make a new exploratory movement upon the other side.

By such side to side movements *L. rubra* can employ the foot as a direction receptor. The shell shades the sensitive region from light directly behind, so that relative intensity of light incidence at either side must be detected by lateral movements of the foot. With a strong light source in front of the animal, the exploratory activity of the foot is greatly intensified and on first emerging there is no attempt to grip the substrate; instead the tip of the foot is raised well clear of the ground and very freely moved about, the tip now extending narrowly, now being pulled back and contracted. Such movements may continue some time before the foot is planted and sustained forward progress is usually not attempted till the animal has swung away from the directly anterior light source.

A behavioural comparison can best be found in a very different animal, the dipteran maggot, which Fraenkel & Gunn (1940) would regard as the classic case of orientation by klinotaxis, 'a directed orientation made possible by means of regular deviations and involving comparisons of intensities at successive points in time'. The tiny pointed anterior end of the maggot has no well-defined photoreceptor. Variation in stimulation must occur as it is drawn in and covered by succeeding segments and then put out again. Thus, just as with the momentary contraction or withdrawal of the foot in *L. rubra* the 'photoreceptive region does not pass straight from one side position to the next, but goes through a series of light intensities which includes the comparative darkness of the contracted position'.

As the shell falls to one side or the other during extension of the foot, a wide shadowed zone is cast around the foot on that side (Fig. 2F). It was at first suspected that regular recumbence of the shell on one side and the other, with alternate steps, would in itself give a rough power of comparison of light intensities, making possible—as it were—a klinotaxis without lateral deviation by the foot. In Fig. 5 is shown a 20 min record of the movements of an animal away from a light source; it will be seen that there is no strictly regular alternation of the shell to right and left sides and that after slumping in one position, there is a tendency to return there for several steps. In addition, the time frequency of light comparison by the shading of the shell would be very low and much more sensitive comparison is in fact possible by the deviations of the foot. A shadowed zone on a particular side must, however, afford the animal a wider sector in which it can move transversely to the light path while still effectively shaded from direct light.

BEHAVIOUR IN DARKNESS: ORIENTATION BY LIGHT

When removed from its site and placed in the dark on a smooth flat surface, *L. rubra* is unable to orient, and crawls about to produce trails of three kinds: (i) about a third of the animals tested in the dark made a short trail of a few millimetres in length, after which they attached by the byssus thread and made no further movements; (ii) a smaller number produced trails that were difficult to follow exactly or to measure, since they were tightly convoluted with continual changes of direction; (iii) the majority produced a strongly convoluted and frequently looped trail, crawling over distances of up to 200 mm in the half-hour period of the experiment. These undirected movements have much in common with the dark behaviour described by Ullyott (1936) in the flatworm *Dendrocoelum*. They show under uniform conditions a certain basal frequency of turning, random in direction. The character of such trails can best be quantitatively represented by expressing against time the rate of change of direction (r.c.d.) in angular degrees per minute. When *Dendrocoelum* were placed in uniform non-graded light, the r.c.d. was found to increase with the intensity of light stimulation. With *Lasaea rubra* in the dark on a smooth surface, we must regard the deprivation of lateral contact as constituting in itself, as illustrated by trails of type (iii), a stimulus of intensity sufficiently high as to produce a r.c.d. equivalent to that shown by animals in light. The character of type (iii) trails and the amount of turning they show do not appreciably alter from the dark condition after the provision of uniform non-direction light (Fig. 3). Ullyott found that *Dendrocoelum* became 'adapted' to the stimulus of light, i.e. the r.c.d. at a given level of illumination fell off with time. With *Lasaea rubra* in the dark, though the stimulus of deprivation of lateral contact appears as high as that provided by light, adaptation was seldom seen: the r.c.d. was not in general lower after 30 min than at the beginning of an experiment. (The high peaks shown in Fig. 3 (1), for a trail made in directional light, fall well within the range shown by many dark trails.)

With uniform ungraded lighting, from the light source of 9·2 candelas, 20 cm vertically above, diffused by a sheet of opal glass, *L. rubra* showed few

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Legend to Fig. 3.

Fig. 3. A. Rose diagrams showing the relative extent of trails produced at various angles: (*a*) aggregated results of experiments on flat surface in the dark; (*b*) results of experiments with a non-directional light gradient, illumination falling from right to left, showing klinokinesis with adaptation. B. Traced records of representative trails produced: (left) on a level surface in the dark, with examples of types (ii) and (iii) referred to above; (right) in experiments using a non-directional light gradient, illumination falling from right to left. C. Histograms showing the characteristics of various types of trail over a 30 min period: (1) in a gradient of lateral light, falling from 9·2 lux; (2) on a level surface in the dark; (3) with uniform light incident from above; (4) climbing a slope of 30° from the horizontal in the dark. Ordinate: degrees angular change of direction; abscissa: time in minutes.

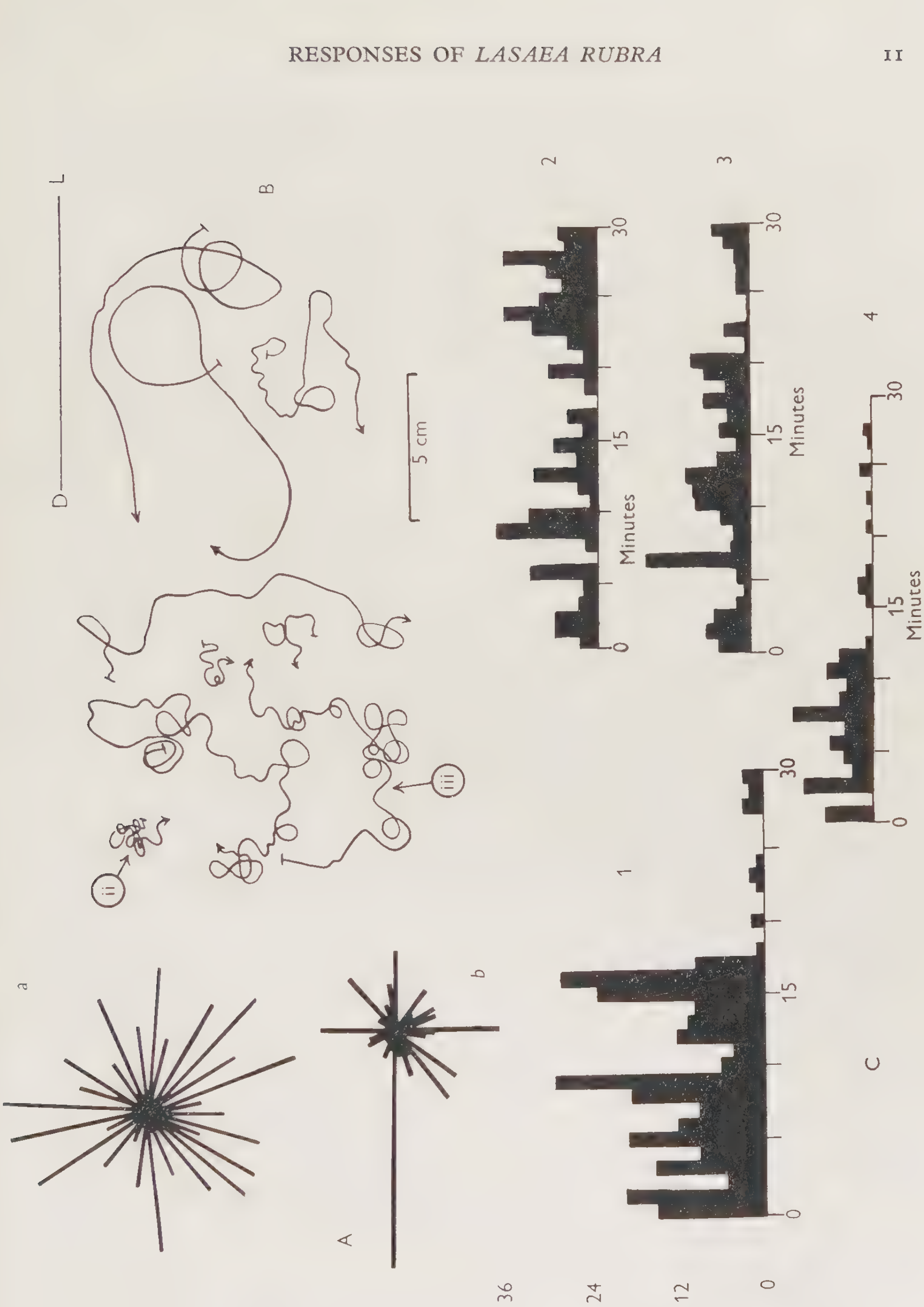

Fig. 3. For legend see opposite page.

or none of the trails of types (i) and (ii); all the animals used were highly active and made long, meandering and looping trails of type (iii). Light provides an augmented stimulus to initiation of movement, though the r.c.d. under the stimulus of light is no higher than with those animals that produced type (iii) trails in the dark. The shape of some trails in ungraded light indicated that some adaptation had occurred after 30 min (see Fig. 3 C (3)).

By various methods (see Ullyott, 1936) a horizontal gradient of light can be projected from vertically above the experimental substrate, so that the animal cannot orient by reference to any light source in the horizontal plane and can perceive only the patch of light directly above it. Such a non-directional gradient of illumination was provided for *L. rubra* by passage of light from the light source placed overhead, through a horizontal 'wedge' formed of a photographic half-plate after graded exposure. Such a situation is the classic one for demonstrating 'klinokinesis with adaptation', an inexact method of orientation by which aggregation can take place without the use of directed light. Change of direction will be longer delayed when the animal adapted to a higher light intensity is moving towards a region of lower intensity. In moving up a gradient towards higher light intensity, increase of stimulus will outrun adaptation and a turning movement, random in direction, will occur sooner. The net progress will thus be towards regions of lower light intensity, though all direct means of orientation are lacking. See, for example, the specimen trails reproduced in Fig. 3 B. The rose diagrams show the relative amounts of movement with respect of the light gradient. 24% takes place within 5° of the gradient towards the dark side. Such aggregation must, however, be an inefficient mechanism in a slow-moving mollusc: effective aggregation by klinokinesis must depend on the ability to move fast and to change direction quickly. *Dendrocoelum*, for example, and *Paramaecium*, which aggregate in this way, move much more rapidly in relation to their size than can *Lasaea rubra*. Optimum conditions in the field are in fact attained by *L. rubra* by orientation of a much more precise kind.

L. rubra responds to directional light by a negative phototaxis. In Fig. 6 A are shown some typical trails of animals placed in a directional light gradient (9·2 lux at *s* to 4·1 lux at *s* 1). Movement is no longer random in direction. In experiments beginning at the lighter side of the gradient, closest to the light source, all the trails show, with greater or less precision, a general direction towards the darker side of the field. With higher light intensities, this is achieved by a relatively straight course with side to side deviations of the foot; with weaker illumination, the trails meander much more widely, and may develop loops (Fig. 6 B).

The light gradients used are shown in Table 1, with the neutral filters as shown. Efficiency of orientation was determined by totalling for each experiment the distances crawled by all the animals used, at various angles to the direction of the light gradient. The results are expressed in the rose diagrams

(Fig. 4) from which the data shown graphically could be further calculated. In the graphs, two sets of values are plotted; for each light intensity the percentage of the total linear movement represented by parts of the trails between $+5^\circ$ and -5° with the line of the light gradient, and similarly the percentage of trails formed at angles of between $+45^\circ$ and -45° with the line of the gradient. With similar rose diagrams (Fig. 3) the randomness of movement in the dark, and movement in a non-directional gradient have already been shown. In these calculations initial or intermediate parts of the trails showing small loops or continued alteration of direction, without sustained directional movement for a length of 1 cm, were disregarded.

TABLE 1. ILLUMINATION WITH THE RANGE OF NEUTRAL FILTERS USED

Density of filter*	Transmission	Illumination at *s* (lux)	Illumination at *s* 1 (lux)
0·1	0·79	7·26	3·23
0·2	0·63	5·79	2·58
0·3	0·50	4·60	2·05
0·59	0·26	2·40	1·02
0·98	0·10	0·92	0·41
2·06	0·0087	0·08004	0·03567
3·0	0·001	0·0092	0·004
4·02	0·000095	0·00087	0·00038
4·8	0·000016	0·000138	0·000060

Illumination of full moon on a clear night 0·2 lux
Illumination of a moonless night 0·0003 lux } (le Grand, 1948)

* All densities referred to here are optical densities $\left(\log_{10}\dfrac{\text{light incident}}{\text{light transmitted}}\right)$.

The trails made at higher light intensities undoubtedly represent klinotactic orientation; but it is not easy to mark an arbitrary distinction between these and the trails at lower intensities, some of which are better regarded as klinokinetic, with random changes of direction achieving orientation by adaptation. The loss of randomness is with increasing stimulation obviously gradual, and it is this power to make regulated deviations in relation to the direction of the gradient, followed by appropriate response, that marks the attainment of klinotaxis. A further calculation reveals what may be described as the 'inefficiency ratios' in such klinotactic and klinokinetic orientation: the total length of the trail crawled was divided by the progress achieved, i.e. the length of the straight line joining the initial and end points of the trail, regardless of its angular direction, and the result expressed logarithmically. With improving orientation at the higher light intensities this will approach zero, though such a value is never attained with photo-orientation alone.

Some measure of the amount of activity of the animals at the various light intensities was obtained by averaging the total length of all the trails obtained with each illumination level, reduced to unit time of 30 min. Too great precision should probably not be assigned to values so derived. They fall

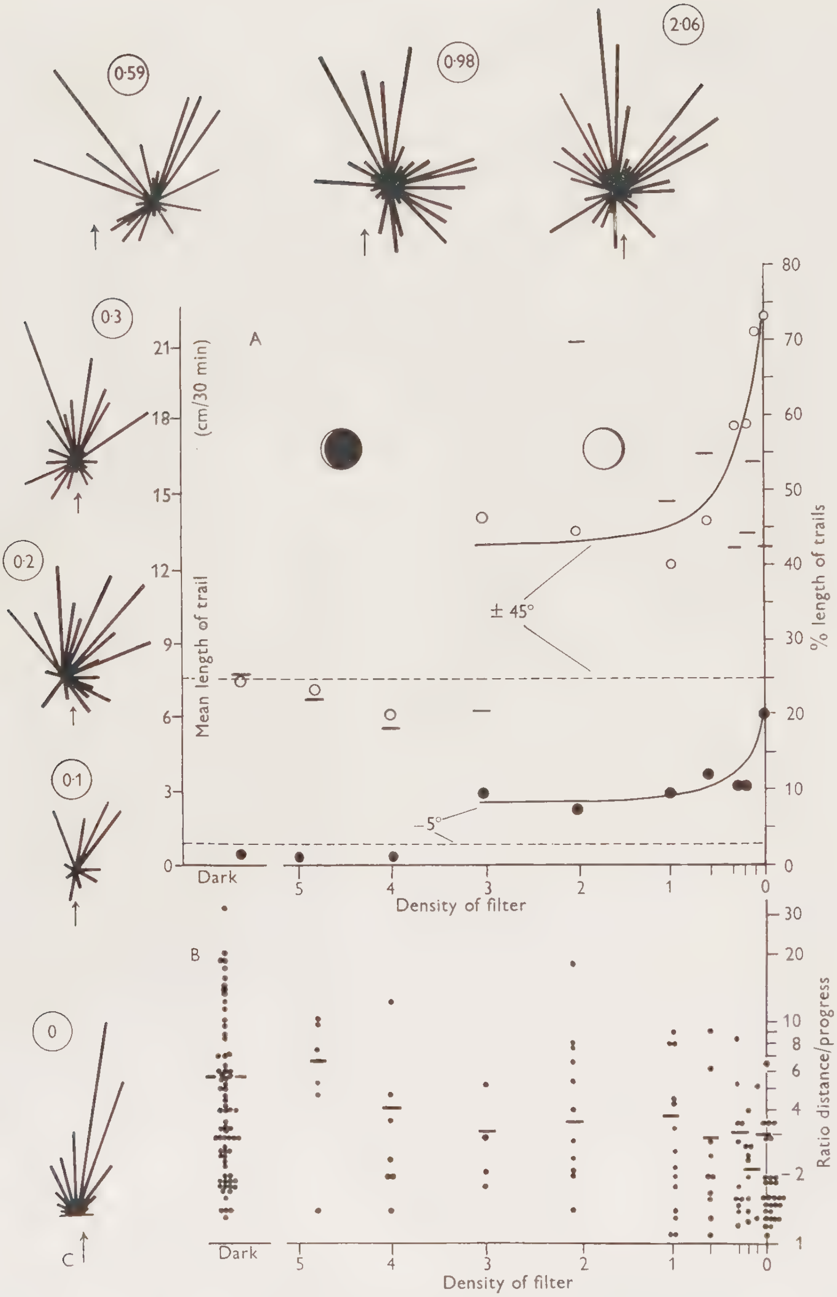

Fig 4 For legend see opposite page.

into two groups. The lower group, at light intensities below 0·01 lux, have a lower total activity, not much greater than that in the dark. Activity strongly increases with illumination from 0·1 lux upwards, with, however, a tendency to fall back at the highest levels of illumination; this last finding is an expression of the greater directness of the trail and the smaller expenditure of wide meanders and loops, at higher light intensities.

Efficiency of orientation, as assessed by the results in Fig. 4, shows three levels. First, using a 9·2 lux illumination, with transmission reduced to one ten-thousandth and below, there is no orientation. Movement at angles within 45° of the light gradients is no better than the random value to be expected with animals in the dark (in one experiment involving only a small number of trails the value falls somewhat below the theoretic random). Above this level of illumination there is a threshold where the values for orientation with the 45° and 5° angles show a strong improvement upon the random level. Orientation is now possible away from the light source and down the gradient; but as shown by their high inefficiency factor, and their form in Fig. 6 B, the trails are of the meandering and looping sort characteristic of a klinokinesis. With an illumination of above 2 lux, orientation finally achieves the character of klinotaxis; trails are much more direct or with smaller meanders (see Fig. 6 A). The curves for orientation both within angles of 45° and 5° show a steep upward trend, towards the values obtained with 9·2 lux. On the graph of Fig. 4 are inserted the values for the illumination of a moonless night and a fine night with full moon (see le Grand, 1948). Photo-orientation is clearly impossible on a moonless night; the threshold for klinokinetic orientation lies at roughly half the illumination of full moon, while the characteristics of the more precise klinotactic orientation are revealed only at illuminations of a twilight order and above.

Legend to Fig. 4

Fig. 4. Results of experiments on photo-orientation. A. Graphs showing the percentages of the total lengths of trails formed between angles of +5° and −5° with the line of the light gradient [●—●]; and between angles of +45 and −45° to the gradient [○—○]. On the abscissa are represented the values for log light transmission, used in the various experiments, 0 corresponding to an illumination of 9·2 lux. The broken horizontal lines show the theoretical values for random movement as on a level surface in the dark, without orientation. The intensity of illumination on a moonless night and on a clear night with full moon is indicated by symbols on the graph (see le Grand, 1948). The short horizontal lines for each illumination represent the mean length of trail formed in 30 min in the aggregated experiments (see left ordinate), and thus give a measure of the level of activity. B. Scatter diagram showing for individual trails at various illuminations the value for the 'inefficiency factor' of distance crawled/progress achieved. Small cross-bars represent mean values. C. Rose diagrams (at the left and upper margins) showing the relative extent of the trails produced at the varying angles from the direction of the light gradient, for different levels of illumination. The illumination is represented by the values in small circles for the filter density (= minus log transmission). The light gradient falls off in the direction of the arrows.

GRAVITY RESPONSES

Efficiency of orientation greatly improves if the substrate is inclined. *Lasaea rubra* is strongly negatively geotactic, and as the angle of the experimental glass sheet was inclined more steeply from the horizontal, the trails (i) became more direct and meandered less and (ii) increasingly took the steepest path.[1]

In moving up a sloping surface, *L. rubra* attaches itself securely by two means: the viscid mucus of the foot is generally sufficient to give it a hold as effective as that of a snail on a steep surface; while at the steepest inclinations, 50° or more from the horizontal the byssal gland secretes a 'safety-line' which is fastened to the substrate at intervals of about 1·5 cm. This is thin and strong, looking like a strand of spider web, laid down parallel to the mucous trail of the foot, and crossing it occasionally if the latter should slightly meander. If the mollusc should then fall off from a steep surface, it will swing freely, still attached by the short available length of free byssus line, instead of falling the considerable distance to the bottom of the slope. By taking contact with the substrate it can at once resume crawling a centimetre or two below the point it had last reached. Such accidents are clearly recorded on the trails as short parallel lengths of double track (see Fig. 5). This safety device must be responsible for the animal's surprising freedom to wander out of crevices and to exist as a freely mobile lamellibranch on rock faces strongly exposed to wave action. Several sorts of bivalve can crawl along the surface; but few can be so apparently defenceless against wave battering and dislodgement as *L. rubra*. The safety line may also be secreted on a flat surface, though it is here much less distinct and, especially where the trails meander considerably, it is not often seen.

In experiments on inclined surfaces in the dark the experimental glass plate was sloped at 10° intervals, at angles of 10°–90° from the horizontal. The efficiency of orienting at 90° to the horizontal edge of the plate was estimated with two curves, as for the light response. The curves of Fig. 5 agree well with the curve of Hovey (1928), expressing the mean angle of upward orientation against the angle of inclination of the substrate. Even at the lowest angle of inclination, *L. rubra* has an orienting efficiency equivalent to that obtained with the highest light intensity used on the flat; and as the angle is increased this efficiency improves greatly. The trails run more directly up the slope; the meanderings are altogether eliminated, so that with slopes of 50° and above, undeviating straight trails were generally obtained, running straight up from the lower edge of the glass plate. Full efficiency is attained at 50°–60° inclination of the slope and thereafter little improvement

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[1] See Fraenkel & Gunn (1940) for discussion of the view that efficiency of orientation on sloped surfaces in many animals is due to postural reflexes, with the use of the statocysts, avoiding the tendency to roll if the angle of ascent of 90° with the horizontal is too far departed from.

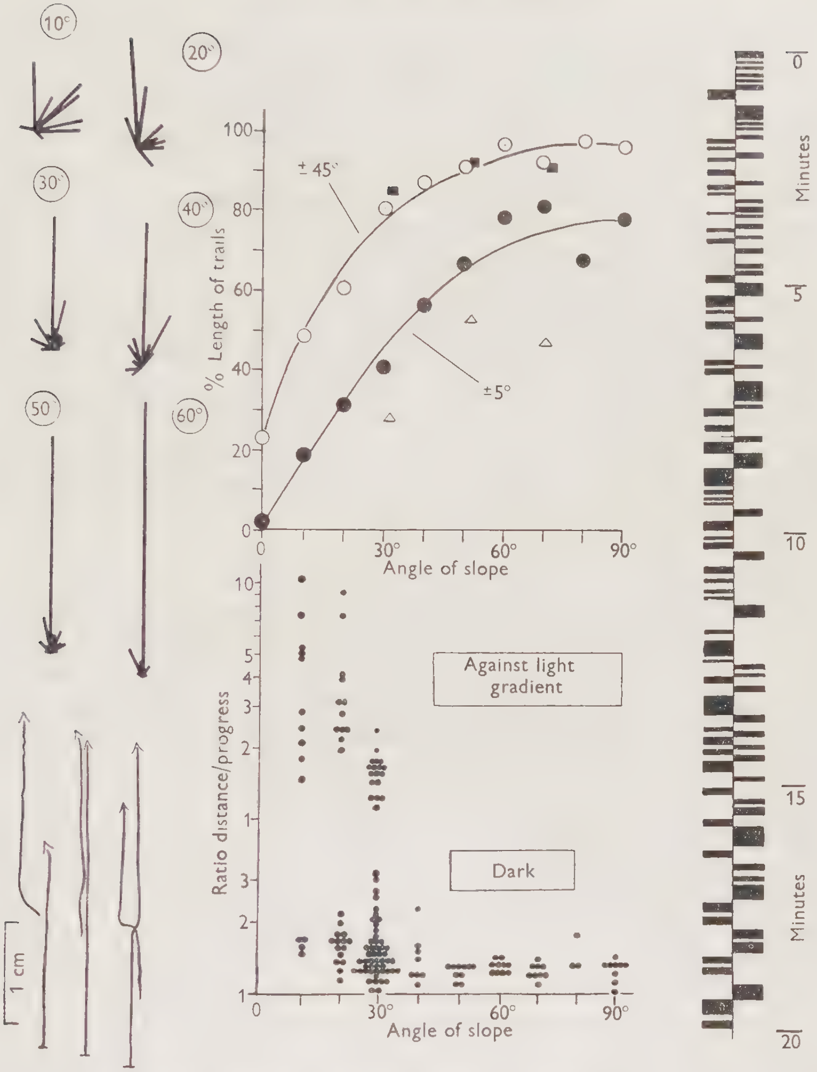

Fig. 5. Graphs showing results of experiments on orientation upon inclined surfaces. Above. Percentages of the total lengths of trails formed between angles of +5° and −5° to a line running directly up the slope [●—●], and between angles of +45° and −45° to such a line. [○—○]. The circles represent experiments with high-tidal animals which were used for most of the work; the triangles and squares show values for the few experiments with animals from low tide. Below. Scatter diagram showing for individual trails in various experiments the values for the 'inefficiency factor' of distance crawled/progress achieved. The lower points are for inclined surfaces in the dark; the upper points are for trails made on inclined surfaces by animals crawling against a light gradient. *Left*. Rose diagrams showing for various angles of inclination of the surface the relative amounts of trail produced at angles to a line running directly up the slope. *Left below*. Portions of trail produced on inclined surfaces after the animal had fallen from the glass plate and—retained by its byssal mooring line—had commenced a fresh trail. *Right*. A record of 20 min movement by a single *Lasaea rubra*, showing the periods of subsidence of the shell alternately to left and right, between 'steps' (see p. 9).

is to be seen. The inefficiency factor (length of trail crawled/distance achieved) falls rapidly to reach unity at the steeper slopes.

In one experiment a comparison was made of the orienting power on inclined surfaces of the reddish brown *L. rubra* from the high-tidal *Chthamalus* barnacle zone (as used in most of these investigations of orientation) and the paler specimens to be found in the low-tidal zone. This was done in view of Morton, Boney & Corner's report (1957) of physiological differences in these two sections of the population, with greater adaptation of the high tidal ones to the harsher conditions of reduced tidal submersion. The results, with low-tidal specimens, shown in the graph of Fig. 5 show little significant difference from the findings with high tidal. The points in the graph for low-tidal animals may appear to suggest a lower efficiency of orientation within 5°. The number of experiments was, however, small; they indicate only that the different positions assumed by the 'high' and 'low' populations on the shore are probably not—to any important extent—the result of striking differences in negatively geotactic orienting behaviour.

Orientation on an inclined surface against a light gradient

Negative geotaxis supersedes negative phototaxis when these two stimuli are so arranged as to work oppositely. Experiments were made in which the lamp previously used was placed above the upper edge of an inclined glass sheet, so that the animal as it climbed both approached the light source and entered into an increasing intensity of illumination. Negative geotaxis was elicited as in the dark, with the same approximation to the vertical of the general direction of the trail, for a given angle of inclination of the glass plate. The appearance of the trails, however, differs from those made at a similar inclination in the dark; they are thrown into frequent meanders at close and rather regular intervals; and there is little if any crawling in a sustained straight line. At 10° and 20° inclination of the glass plate there was much more tendency to begin by making an irregular and apparently unoriented trail, and to continue in this fashion with delay in beginning to orient. Those animals that oriented almost all took wide meandering divergences, though the conventionalized angle of steepness of the trail was very similar to that of trails on correspondingly steep surfaces in the dark. The inefficiency factor of length of trail crawled/distance achieved was, however, considerably increased. With animals climbing a 30° slope against the light, a few trails were relatively straight and unconvoluted; the majority meandered continuously, though with shorter and more regular divergences than at 10° and 20°. The path followed by these trails shows that the animal never crawled for long directly towards the light source, nor was either of its sides continually exposed for more than a short time to the full incidence of lateral light. The frequent changes of direction enabled the previously exposed side to be regularly shaded. The side for the time being uppermost, i.e. exposed to full lateral illumination could not, however, be shaded from light by the shell as is possible on the flat. The heavy weight of the shell and body in climbing will always tend to slump downwards over the side already away from the light.

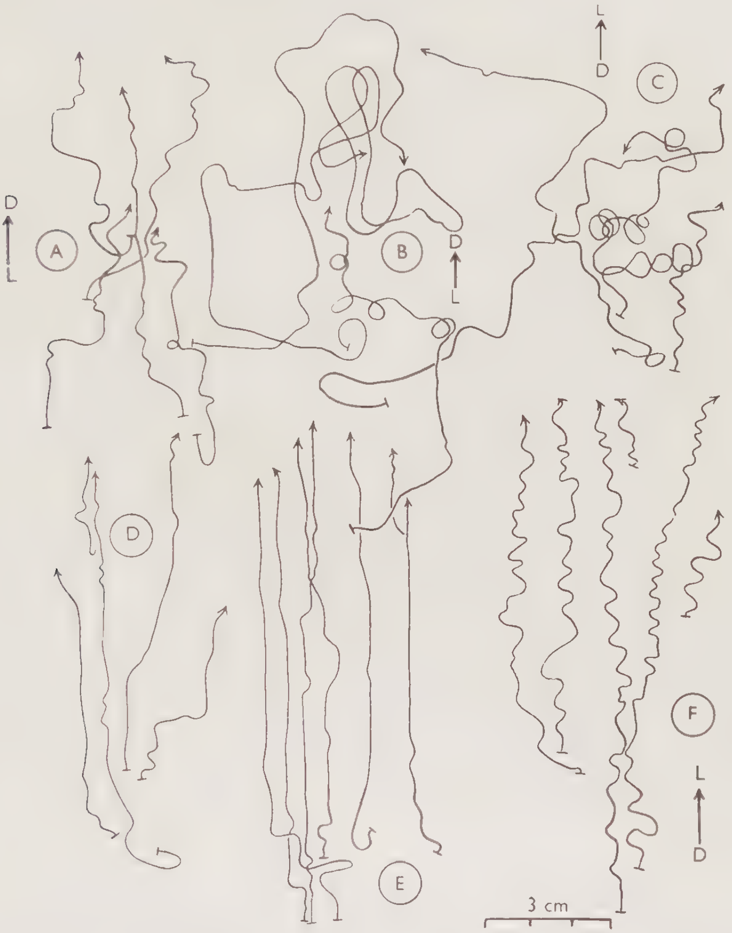

Fig. 6. Representative specimen trails with various orienting stimuli. For each group the direction of the stimulus producing orientation would be represented by a line running directly up the page. (Rather more than half natural size). A. Photoklinotactic trails in a gradient of illumination falling from 9·2 to 4·1 lux over 9 cm. B. Photoklinokinetic trails in a gradient of illumination falling from 0·080 to 0·036 lux over 9 cm. C. Trails produced in climbing a surface inclined at 30° to the horizontal, *towards* an illumination of 9·2 lux at the end-point. D. Trails produced in climbing a surface inclined at 30° to the horizontal, in the *dark*. E. Trails produced in climbing a surface at 60° to the horizontal in the *dark*. F. Trails produced in climbing a surface inclined at 30° to the horizontal, *towards* an illumination of 9·2 lux at the end-point.

RESPONSES TO LATERAL CONTACT

The normal habit of *Lasaea rubra* is to nestle in a narrow crevice or depression affording it a maximum of lateral contact. When removed from such contact, and placed on a horizontal surface in the dark, the animal's typical reaction is to wander about continuously; and when brought in contact with a small depression or cavity in the substrate it will accept it at once. The wandering behaviour of the animal deprived of its refuge is of an orthokinetic type; it differs from a kinesis with light in that the animal is not subject to the orienting stimulus until it finds a crevice and settles down. There can be no gradient of stimulus, and orientation cannot be assisted by adaptation; the refuge is attained by random wandering in a much deviating and convoluted trail. Fraenkel & Gunn (1940) call such behaviour a low *thigmo-kinesis*, since 'a low intensity of stimulation by contact leads to high activity'. In default of any other refuge, two or three *L. rubra* will aggregate together in a small heap, attaching to each other with byssal threads (an example of the so-called 'idiothigmotaxis' of Krumbiegel, 1932).

In the first experiment (Fig. 7 B) shells were placed on a horizontal Perspex plate in the dark, equidistantly between round holes 3 mm in diameter drilled at intervals of 2 cm. The animals 'found' these holes in the course of unoriented wandering, and a specimen coming in contact with the edge of a hole would at once enter it, and if, as in this case, the lumen was narrow enough to afford an appreciable increase in lateral contact, would remain there and secrete a byssus. Lateral contact is presumably not detected directly by the shell, but by the extrusion of the foot and of the wide margin of mantle that comes in touch with the substrate as the valves are relaxed. Similar results were obtained by distribution on the surface of the plate at the same intervals as the holes, of empty *Chthamalus stellatus* shells, either lying on their sides with the base widely open, or tilted so as to allow a narrow entry at the base.

	Holes	*Chthamalus* shells
Animals exposed	33, 32, 10	33, 9, 16
Animals in refuge after 1 h	8, 15, 7	22, 5, 9

From Fig. 7 B, showing the trails laid down in a typical experiment, it is clear that of those animals in refuges, all had reached their shell or hole without previously touching any other; every animal once within a refuge had stayed there, and that those remaining without refuge had never in the course of the experiment made contact with a shell or a hole.

At the point of entry into a randomly found hole, a short vertical descent is necessary from the flat surface. This would appear to be of a thigmotactic nature (as distinct from random thigmokinesis): contact with the concave interior of the hole guides the animal during its deeper entry into the refuge. Such a thigmotaxis will reverse the normal negative geotactic response.

A similar change of the general behaviour pattern in response to irregularities in the substrate has already been described by Fraenkel (1927) for the high-tidal periwinkle *Melaraphe neritoides*. This snail passes through transverse crevices on its upward climb, crawling into the bottom of a crevice and emerging by crawling out upside-down along its roof. The normally negative phototaxis is here reversed.

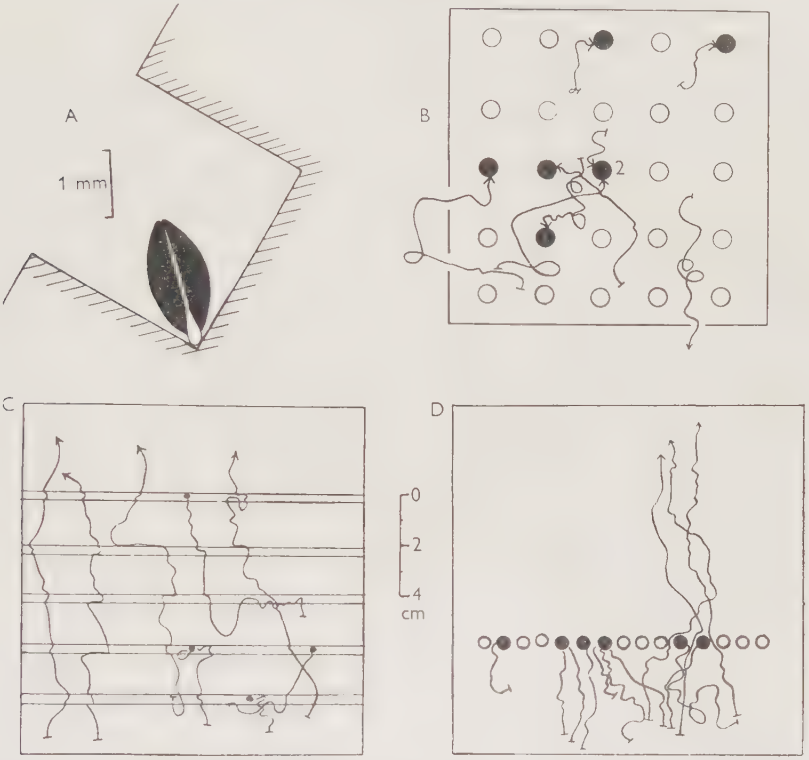

Fig. 7. A. Diagram showing typical position assumed by *Lasaea rubra* crawling along a groove cut in a Perspex sheet, with the maximum thigmotactic stimulus afforded by either of the angles. B. Diagram showing the trails of six *L. rubra* that have arrived at a refuge, crawling in the dark, with random change of direction over a smooth, level surface studded at regular intervals with holes. Black circles represent occupied holes. C. Representative trails of *L. rubra* climbing up a Perspex sheet inclined at an angle of 30° and with its surface interrupted at intervals by transverse grooves. D. Representative trails of *L. rubra* climbing a glass sheet inclined at an angle of 30°, with a barrier of a line of *Chthamalus* barnacle shells. Those animals that made contact with a barnacle were arrested and took refuge in the shells shown as black circles. Those that continued to the top of the sheet had made no contact with barnacle shells.

Thigmotaxis opposed to the stimuli of light and gravity

The lateral contact provided by a crevice or a depression will normally in *Lasaea rubra* supersede the usual responses to both light and gravity.

Experiments were made with Perspex sheets, inclined in the dark at an angle of 30° to the horizontal. The upward path of the negatively geotactic animals was interrupted at intervals of 2 cm by four transversely cut horizontal grooves, of square cross-section and measuring 3 mm along the side. Animals were placed in a row at the lower edge of the plate and allowed to climb. In each of the six experiments, a small proportion of animals were, for the 1 h duration of the experiment, halted by the first groove. A few reached the second groove and remained there. The majority in each experiment passed across all the grooves and continued to climb, some without apparent interruption, others wandering laterally for some distance along one or more of the grooves before emerging and continuing their climb. Of those that remained in grooves to the end of the experiment, none appeared to secrete a byssus. Lateral movement with a groove was generally along one or other right-angled corner, and appeared to be directed by a thigmotactic response that for a time superseded negative geotaxis, though in the lower angle the gravity stimulus would be removed and in the upper angle resumption of climbing might be impeded by the difficult contour. With long grooves of 3 mm cross-section, the lateral contact afforded would seem to be insufficient to restrain for long the tendency to climb.

A much more effective barrier is provided by a row of empty *Chthamalus stellatus* shells near the lower edge of the Perspex plate separated by intervals of 3 mm, sufficient to allow a bivalve to pass through. As shown in Fig. 7 D from a typical experiment, all those animals that came into contact with a barnacle shell crawled into it and showed no further upward climbing. Only those continued to crawl upwards that had passed between two shells without touching either.

In further experiments a light stimulus was opposed to that of lateral contact. A horizontal Perspex plate was perforated with holes of 3 mm diameter set in seven rows of fifteen holes at 5 mm intervals. These holes were strongly lighted from underneath the plate by the lamp previously used, while the rest of the plate was painted underneath with black marine-varnish, so that the experimental surface on top of the plate was kept dark. A thin glass plate was placed beneath, to provide a transparent floor for the holes. Forty-five animals were randomly distributed on the lower half of the plate and a low stimulus of directional light was provided, much weaker than light in the holes. Under this stimulus the animals moved with wide meandering trails across the plate towards the area of the holes. After 8 h, out of a total of forty-five animals, thirty-four were within holes, a proportion very comparable to those that found refuge in unlighted holes or barnacle shells. Contact with the edge of a hole would appear to release a thigmotactic behaviour resulting in entry to the hole regardless of the opposing stimuli of light or gravity.

In another experiment a horizontal Perspex sheet was set up in the dark, varnished black underneath, and pierced with forty holes 3 mm across. Two *L. rubra* were placed in each. The plate was inspected after an hour in the dark and the animals that had emerged from holes were counted and replaced. The holes were then brightly illuminated from beneath and the plate inspected again after a further hour.

Number of animals originally in holes	80
Number emerged after first hour dark and then replaced	15
Number emerged after second hour lighted	9

Of the dominance of thigmotaxis over phototaxis we have already an example in the literature, the short study of the responses of newly settled *Hiatella arctica* spat by Hunter (1949); here the animals settled in crevices provided by glass slides fixed together at an angle, even though these crevices were the most brightly lighted spots.

DISCUSSION: MAINTENANCE OF POSITION ON THE SHORE

The movements and orientation of *Lasaea rubra* from the *Chthamalus stellatus* zone, as studied here, appear to be directed to securing and maintaining the position of the population on the upper shore, and within that level to acquiring crevices, empty barnacle shells or other lodgements protecting the animals from detachment by waves and currents and from desiccation and the actions of direct light. As a dimyarian eulamellibranch of 'normal'-looking ovoid shape, *Lasaea rubra* would at first appear to be strikingly little adapted for life on wave-exposed rock faces. It has made none of the sacrifices to semi-permanent byssal attachment with alteration of symmetry undergone, for example, by the Mytilidae. Its first advantage is its minute size (see Morton, Boney & Corner, 1957). Its shell, moreover, when viewed edgewise is lentiform and well streamlined against impact of moving water.

Lasaea lacks the frail shell and obese appearance of its relative *Kellya suborbicularis*, which is much more confined to low-tidal crevices and much less peripatetic; and there is no suggestion of the wedge-shaped shell found in the burrowing Erycinacea such as *Montacuta ferruginosa*. The *Lasaea* shell is indeed of an ideal construction for lying submerged in, and filtering from the merest film of splash. There are three other important adaptive features, an extensible foot that can provide viscous attachment to the substrate, a byssal gland that can secrete an attachment line where needed, and a forward facing inhalant siphon, serving as an anteroceptor.

L. rubra may from time to time creep about on open rock surfaces and can readily alter its fixed position. In spite of the precaution of a safety line, the result of movements of disturbed water would tend to carry dislodged shells downshore. The dominant orientation reaction shown by *L. rubra* when removed from a crevice is that of negative geotaxis, by which it will climb even against a gradient of light to which at other times it would respond negatively. Gravity must be the most continuously sustained stimulus to which *L. rubra* is exposed when out of its lodgement; and it is the stimulus most efficiently responded to, forming, so to speak, the 'coarse adjustment' mechanism, for large-scale maintenance of position. Negative phototaxis is effective only on relatively level surfaces in the absence of a strong gravity stimulus. It serves as an alternative coarse adjustment mechanism, not with the same precision as the gravity response, but nevertheless with the efficiency of a klinotaxis at the illumination of a moonlit night. Such a reaction should produce aggregation in the darkest places which will be crevices or barnacle shells or depressions suitable for nestling. The lowest threshold for photo-orientation is somewhat higher than the illumination level of a night without moonlight; and at the lower levels of detectable light, orientation is chiefly by the inefficient mechanism of klinokinesis. A low level thigmokinesis produces random wandering with very convoluted trails in the absence of a light or gravity stimulus; and once the edge of a narrow depression or crevice is randomly located, a thigmotactic response carries the animal into its narrow confines, even in opposition to the normal responses to gravity and light. Thigmotaxis is a very strong response in *L. rubra* and provides the 'fine adjustment' mechanism by which a suitable crevice is ultimately secured. Preference for lateral contact, and perhaps in part avoidance of light, may constitute a 'token stimulus' leading the animal to a place of shelter whose real advantages are, however, protection from dislodgement by waves or currents, from desiccation in a dry atmosphere and perhaps from predation.

L. rubra is seldom found singly but usually in clusters of two or three large shells with many half grown or newly born beside them. This aggregation may represent a special case of thigmotaxis; but another mechanism must be considered in the Erycinacea, that of chemotaxis. The anterior position of the inhalant siphon offers a preadaptation for direction finding by chemotaxis, and orientation towards other animals may be a rather regular faculty of the commensal Erycinidae and Galeommatidae. In *Montacuta ferruginosa* with *Echinocardium cordatum* there is a well-developed chemotaxis towards the host. I shall describe this elsewhere. In the non-commensal *Lasaea rubra* there is another possibility of chemo-orientation, an 'homoio-chemotaxis' assisting the animals to find their near neighbours at the final stage of aggregation. A hundred or so animals scattered in a Petri dish of sea water overnight will usually resolve themselves in up to a dozen heaps attached together by the byssus. In the investigation of light and gravity orientation, it was first necessary to know to what extent, if at all, the movements of *L. rubra* were influenced by the detection of others of their kind at close range. From a study of all the recorded trails, with animals distributed at 2 cm apart or more, there was no significant evidence of influence of one animal on another. Trails on a dark, a lighted, or an inclined surface, presented the same apparent randomness with respect to any other animal as they did with respect to a given compass direction when a single animal was studied alone. In the light and gravity experiments reported here any effect of the animals upon each other appeared to be quite subdued by the stronger orienting stimulus. Yet with animals spaced as closely as 1 cm apart, there appeared instances of aggregation that seem anomalous on any theory of complete randomness. For example, in one experiment with a perforated Perspex sheet, animals were found to aggregate in one hole in a group of as many as seven, in others in fours and threes. Statistical investigation of the randomness of aggregation at very short distances must, with the general subject of chemotaxis in Erycinacea, be reserved to a later paper.

L. rubra of the low tidal zone appeared to show an essential similarity in their orienting behaviour, including that of negative geotaxis, with the high tidal ones. Low tidal *L. rubra* are less well adapted to withstand the intermittence of submersion of the upper shore, and it may be these physiological disabilities that set an upper limit to the distribution of the pale forms. Whether there may be genetical differences in the two sections of the population is not known. The lower limit of the upper shore population would tend to be maintained by their upward crawling tendency. The upper limit, about that of the upper barnacle line, must be imposed by the short duration of submersion there, with the low humidity of the atmosphere and the difficulty of crawling for any great distance on a dry substratum. *L. rubra* in the laboratory will sometimes crawl out of water on to a damp surface but never out of a saturated atmosphere. Its upper limit is quite sharply marked with no gradual falling off either in numbers or in mean size. Morton *et al.* (1957) have already mentioned the ecological advantages of a high level shore habitat to a mollusc of warm temperate distribution, reaching the northern limit of its range in Great Britain, and breeding in summer. It appears to prefer the maximum warmth of the sun on the substrate, consistent with the avoidance of desiccation; to both these requirements, the pattern of its orienting behaviour effectively contributes.

It is a pleasure to record my appreciation of the kindness and help given by the Director of the Plymouth Laboratory, Dr F. S. Russell, F.R.S., and by his staff, especially Dr E. J. Denton, for whose ready assistance with apparatus and discussion I am greatly indebted.

SUMMARY

The responses of the small bivalve *L. rubra* to light, gravity and lateral contact have been studied in relation to its orientation and maintenance of position on the shore. In the dark, on a flat surface, or in uniform light, *Lasaea* crawls freely about with meandering unoriented trails. At about half the illumination of full moon, orientation by klinokinesis with adaptation becomes

possible, rising by twilight to a negative photoklinotaxis by which darker crevices and refuges are found fairly directly. On a sloping surface *Lasaea* will crawl upwards, more directly as the slope is increased, and its negative geotactic behaviour will supersede negative phototaxis, so that it will crawl upwards even against a light gradient. As soon as chance contact is made with a small hole or crevice, an empty barnacle shell, or a groove affording lateral contact, both the light and gravity reactions are superseded: the animal will crawl downwards into a hole or enter it against a gradient of bright light from a dark surface. It is suggested that in the natural habitat negative geotaxis provides a coarse adjustment to the securing and maintenance of position, while the reactions to light and lateral contact give an increasing precision in the securing of shelter with protection from wave action, light and desiccation.

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SPECTRAL COMPOSITION OF THE LIGHT OF THE LANTERN-FISH, *MYCTOPHUM PUNCTATUM*

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(Text-figs. 1–3)

Relative spectral emission curves are available for the lights of many invertebrate animals, but none exists for fish. It seems likely that many bony fish use their photophores to signal to one another. Information about the spectral composition of fish luminescence is desirable to permit comparisons with the spectral sensitivities of fish eyes, to enable calculations to be made of luminous intensities, and to allow estimates to be made of the rate of attenuation of such lights in sea water. To further these ends, measurements were made of the spectral composition of the luminescence of the lantern-fish, *Myctophum punctatum*.

MATERIAL AND METHODS

The lantern-fish *Myctophum punctatum* Rafinesque is a pelagic species that executes diurnal migrations to the surface at dusk. Specimens were collected by R.V. 'Sarsia' at three stations: 46° 57′ N., 60° 58′ W., 4 June 1959; 46° 42′ N., 6° 09′ W., 5 June 1959; 47° 01′ N., 5° 55′ W., 7 June 1959. The fish were attracted to the side of the ship at twilight by means of a floating lamp submerged just below the surface. They were caught in hand-nets and transferred to a container of sea water on deck. Myctophids do not survive long in captivity, and the animals were used as soon as possible after capture.

Myctophids possess a series of photophores on the lower surface of the head and trunk. These light up spontaneously, and bright luminous flashes are also evoked by tactile stimulation of the fish.

The spectral composition of the light was determined by means of coloured filters and photomultiplier tubes (Fig. 1). The fish was placed in a black vessel which fitted into a black box. Above the box was a round aperture. Over this aperture was placed a thin cover-glass at 45° to the vertical axis. One photomultiplier (vertical) was placed directly over the cover-glass and the aperture; a second photomultiplier (horizontal) was placed at right angles to the vertical axis at one side of the cover-glass so as to catch reflected light from the latter. Between the cover-glass and the photomultiplier there was a disc, capable of being rotated, and containing a series of coloured filters which could be interposed between the cover-glass and the vertical photomultiplier. The vertical photomultiplier detected the light which passed through the filters; the horizontal photomultiplier monitored the light intensity for each recording made with the other photomultiplier.

The photomultipliers were E.M.I., types nos. 6685 (vertical) and 6260 (horizontal). Both types are most sensitive in the blue region of the spectrum, and sensitivity falls off rapidly above 500 mμ. The spectral sensitivity of photomultiplier tube type no. 6685 was determined by the National Physical Laboratory; the spectral sensitivity curve is given elsewhere (Fig. 2, Nicol, 1958*a*).

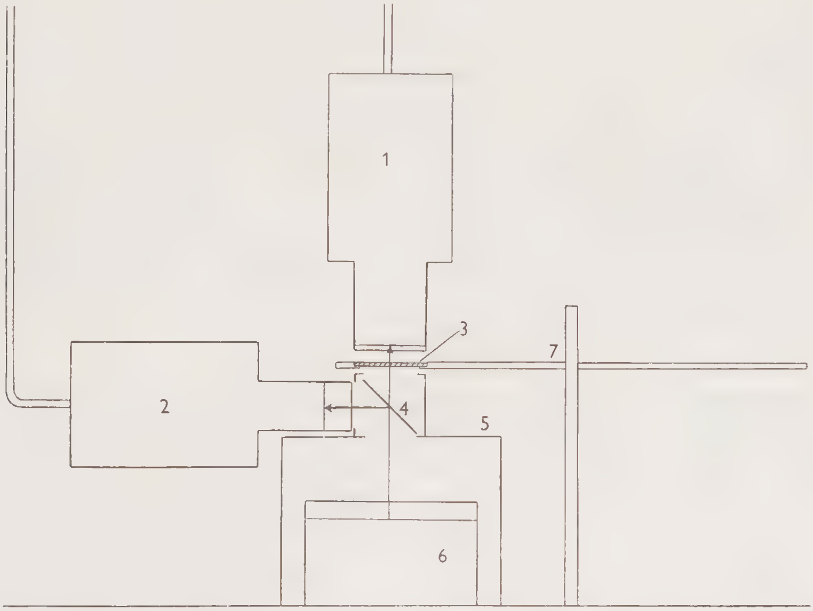

Fig. 1. Diagram of apparatus. 1, vertical photomultiplier type no. 6685. 2, horizontal photomultiplier type no. 6260. 3, filter. 4, cover-glass. 5, black box. 6, black vessel, holding sea water to contain the fish. 7, rotating disc. Arrows indicate light-paths.

Each photomultiplier was connected to a cathode-ray oscilloscope through a d.c. amplifier. Vertical deflexions of the spot on the face of the tube were photographed on moving paper. Current for the photomultipliers was provided by two stabilized power packs. Noise was filtered off by means of a 0·1 μF condenser placed across the input of each oscilloscope.

Filters were Chance OX 1 (u.v.), OV 1 (purple), and Ilford 601 (violet), 602 (blue), 603 (blue-green), 604 (green), 605 (yellow-green), 606 (yellow), 607 (orange), 608 (red), 609 (deep red). The spectral transmission of these filters was measured in a spectrophotometer. Representative transmission curves may be found in manuals of Chance Bros., Ilford Ltd., and curves for $S_\lambda T_\lambda$ (sensitivity of photomultiplier type no. 6685 × transmission of the filters) in a previous paper (Nicol, 1957).

A lantern-fish was introduced into the box and stimulated by gently squeezing it. The response through a given filter and the monitored response were recorded, and this procedure was repeated several times with each of the filters. A fish flashed repetitively under this treatment, and each record showed a number of flashes, some of optimal size for measurement, some too bright and off screen, and some very small and difficult to measure. Representative records are shown in Fig. 2. The deflexions obtained with filters transmitting long wavelengths, viz. 606, 607, 608 and 609, were small and difficult or impossible to measure.

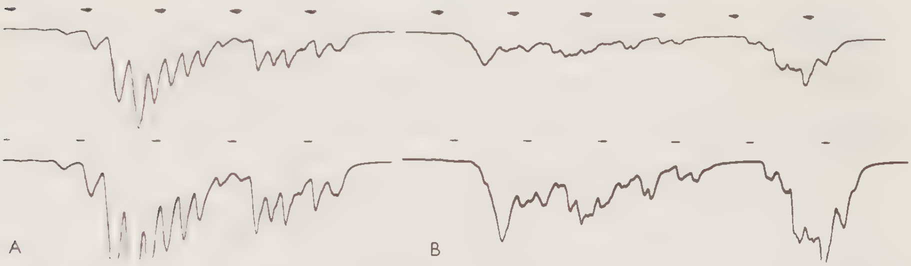

Fig. 2. Recordings of luminous responses. A, two left-hand records. Above, response recorded through filter 603, below, monitored response. B, two right-hand records. Above, through filter 602, below monitored response. Downward deflexions of traces are luminous responses. Time scale 1/sec.

The extent of the deflexions on each record, when possible, was measured. The records obtained with the monitoring photomultiplier were used to correct the records obtained with the filters and the vertical photomultiplier, so as to compensate for differences in the intensities of the response. All records obtained with filters were thus scaled to the same initial intensity. Means of the corrected records for each filter were determined. Let these values be R_X, where X refers to a given filter.

Curves were plotted for the products of the sensitivity of photomultiplier type no. 6685 (S_λ) times the transmission of the filters (T_λ), against λ. The area of each of the curves is

$$\eta_X = \int_{320}^{700} S_\lambda \, T_\lambda \, d\lambda.$$

The mean representative wavelength for each curve was estimated from the vertical axis bisecting the area ('centre of gravity' of the curve).

Relative spectral emission at the representative mean wavelength for each filter was calculated from

$$R_X/\eta_X = Q'_X.$$

From the values for Q'_X a spectral emission curve was constructed (first approximation). Let the relative spectral energy levels on the curve be E'_λ. With these values, a correction was applied to compensate for the wide transmission bands of the filters. A further series of curves was constructed for $E'_\lambda S_\lambda T_\lambda$

$$\zeta_X = E'_\lambda S_\lambda T_\lambda.$$

Ratios were then obtained for each filter

$$\rho_1 = \zeta_X / \zeta_{602}.$$

Similar ratios were determined for measured responses

$$\rho_2 = \frac{R_X}{R_{602}}.$$

The ratios $\rho_3 = \rho_2/\rho_1$, were then used to correct the points on the first spectral emission curve

$$\rho_3 Q'_X = Q_X.$$

A second curve was drawn to fit the points Q_X.

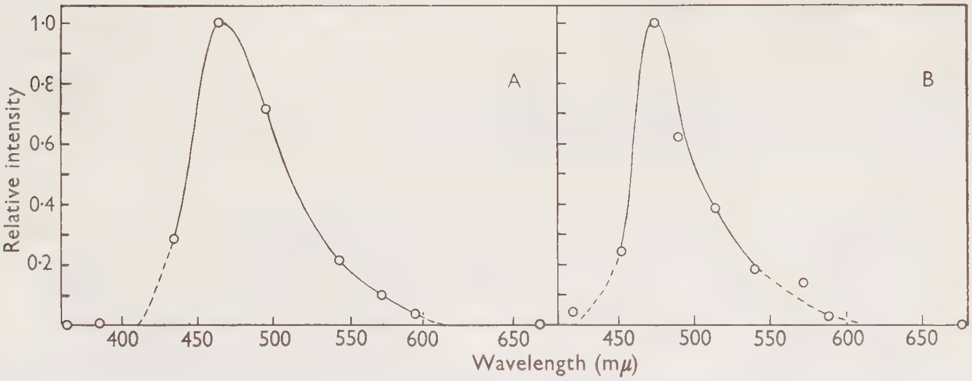

Fig. 3. Relative spectral emission curves for the light of *Myctophum punctatum*. Left (A), uncorrected curve. Right (B), corrected for wide band-width of the filters.

RESULTS

A first approximate curve (filter values Q'_X) is shown in Fig. 3A, and a corrected curve in Fig. 3B. The light is blue in colour and has a spectral range from about 410 to 600 mμ. Maximal emission lies at about 470 mμ.

These results pertain only to the light emitted by the photophores. Myctophids also possess a special light-organ, known as the 'caudal gland', on the caudal peduncle. The 'caudal gland' lights up independently of the other photophores. Its light appears blue to the eye; determination of the spectral composition was not attempted.

DISCUSSION

The lights of luminous fishes have been variously described as white, blue, blue-green, green or yellow. The majority appear to be blue or blue-green (Harvey, 1955). It is likely that several quite dissimilar chemiluminescent mechanisms are involved in the production of light by different fishes, and it is not unexpected that the lights should have different spectral characteristics. *Mycotophum* produces light intracellularly, within photophores. *Searsia*, a deep-sea species, releases a blue-green luminous secretion (Nicol, 1958*b*). *Malacocephalus laevis*, believed to owe its light to luminous bacteria, has a blue-green luminescence. Luminous bacteria, cultured from this fish, emit light having a spectral range of 430–638 mμ, and a maximum at 510 mμ.

Elsewhere I have given estimates of the intensity of the light of *Myctophum punctatum* (Nicol, 1958*b*). According to these estimates, radiant flux ranges from $0{\cdot}1 \times 10^{-9}$ μJ to 52×10^{-9} μW/cm^2 receptor surface at 1 m distance. Since a relative spectral emission curve for *Myctophum*-light was not then available, the emission curve for blue *Chaetopterus*-light was employed in the calculation. This curve is very similar to that for *Myctophum*-light, and the subterfuge now appears justified.

The photophores of myctophids have specific patterns, and it is not unlikely that they are used as intraspecific signals, during mating, schooling, or other social activities. Denton & Warren (1957) have shown that *Myctophum punctatum*, among other deep sea teleosts, possesses a golden-coloured retinal pigment (chrysopsin). The spectral characteristics of the absorption curve for this pigment are rather similar to those for the spectral emission curve of luminescence.

I wish to thank Dr E. J. Denton for helpful advice, and Mr R. G. Maddock for technical assistance.

SUMMARY

Measurements were made of the relative spectral energy in the light of the lantern-fish *Myctophum punctatum*. Light emission extends from about 410 to 600 mμ, with maximal emission at about 470 mμ.

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STUDIES ON THE GROWTH OF MARINE PHYTOPLANKTON

III. *PROROCENTRUM MICANS* EHRENBERG

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(Text-figs. 1–7)

The last of the organisms to be studied in this series was chosen as a representative of the Dinophyceae. The treatment of *Prorocentrum micans* Ehrenberg has been similar to that of *Asterionella japonica* Cleve & Müller ex Gran (Kain & Fogg, 1958*a*) and *Isochrysis galbana* Parke (Kain & Fogg, 1958*b*). The present paper includes a discussion of the results for all three organisms in the light of work by previous authors.

MATERIALS AND METHODS

The strain of *Prorocentrum micans* used originated from the Plymouth collection (No. 97). It was freed of bacteria by the method of phototaxis (Droop, 1954). Individual cells were picked out after they had traversed six 9 cm Petri dishes of sterile medium. For some experiments the original unialgal culture was used and for others the bacteria-free culture.

The methods used in culturing the dinoflagellate were similar to those used for *Asterionella* (see Kain & Fogg, 1958*a*). Pyrex glass tubes (15 × 2·5 cm) plugged with cotton wool were used as culture vessels and immersed in a constant temperature water bath at 20° C with incandescent lighting providing 5000–7000 lux.

The basic media used were Erdschreiber (Føyn, 1934), AK (Kain & Fogg, 1958*a*), AQ_N (based on natural sea water) and AQ_A (based on artificial sea water). Medium AQ was the same as AR (Kain & Fogg, 1958*a*) but without sodium silicate or tris(hydroxymethyl)aminomethane ('tris'). Soil extract, at 20 or 50 ml./l., was usually added to this medium and in all later experiments cobalamin, at 0·1 mμg/l., was included. In addition Provasoli's vitamin solution S3 (Provasoli, McLaughlin & Droop, 1957) was added on occasion. A few experiments were made in medium BD which consisted of natural sea water enriched with nitrate, phosphate and ferric chloride at the same concentrations as in AK, with twelve vitamins (Table 1) and 50 ml./l. of soil extract. Finally medium BE was developed. It was based on natural (BE_N) or artificial (BE_A) sea water and the usual nitrate and phosphate enrichments with the addition of the trace elements and ethylenediamine tetra-acetic acid (EDTA) as in AQ but contained also glycylglycine, at 4 mM and twelve vitamins (12 V). Media were autoclaved at 15 lb./sq.in. for 1 min.

Growth was estimated solely by cell counts, as the large cell size and low population density prevented the use of optical density measurements. The same factors also precluded the use of the usual haemacytometer slides and at first the Utermohl technique (Lund, 1951) was used, all the cells in the sample being counted with an inverted microscope. Later a counting cell was constructed, suitable for use with an ordinary microscope and taking 0·5 ml. of culture. A grid of lines at 1 mm intervals on an area of 1 cm^2 was drawn on a Perspex slide by a sharp knife fixed to the tube support of a microscope. The slide was moved in relation to the knife by means of a mechanical stage, the micrometer scale of which was used to determine the position of each line. The depth of the cut was controlled by the focusing mechanism of the microscope. The grid was surrounded by Perspex walls, ground to a thickness of 0·5 cm, with four channels for the escape of excess liquid. At least 500 cells were counted to obtain an estimate of cell concentration. The distribution of cells on the grid was not quite random, there being a slightly greater concentration at the centre. Allowance was made for this if the whole grid was not scanned.

TABLE 1. THE CONCENTRATIONS IN THE MEDIA OF THE TWELVE VITAMINS (12V) USED

	μM		μM
Thiamin	0·5	p-Amino benzoic acid	0·05
Riboflavine	0·01	Inositol	1·0
Pantothenic acid	0·2	Biotin	0·002
Nicotinic acid	0·001	Folic acid	0·005
Pyriodoxine	0·01	Adenine	0·01
Cobalamin	0·0001	Guanine	0·01

EXPERIMENTS

Growth

An example of the growth curve of *Prorocentrum* in bacteria-free culture is shown in Fig. 1. There was sometimes a lag of about 2 days. Under optimum conditions the relative growth constant *k* in the exponential phase was 0·3 $\log_e$ units/day, corresponding to a division nearly every 2 days. Growth later became slower and the maximum population reached was usually about 50 cells/mm^3 though 80 cells/mm^3 has been recorded.

Nitrogen supply

Bacteria-free *Prorocentrum* was grown in a series of concentrations of potassium nitrate in medium BD from an inoculum washed in sterile sea water. Cell counts were made after 21 days and the cell crop in each culture calculated by subtracting the mean cell concentration in the controls from that in the relevant culture. The cell crop in Fig. 2 is thus an expression of the response to the added nitrate, as distinct from that in the natural sea water or stored in the cells. Fig. 2 also shows the values for the added nitrate divided by the cell crop obtained from it. These do not necessarily correspond to the nitrogen contents of the cells. All except the highest (2 mM) concentration gave similar values, nitrate being evidently limiting, and the mean requirement was 19 $\mu\mu$g-atoms N/cell.

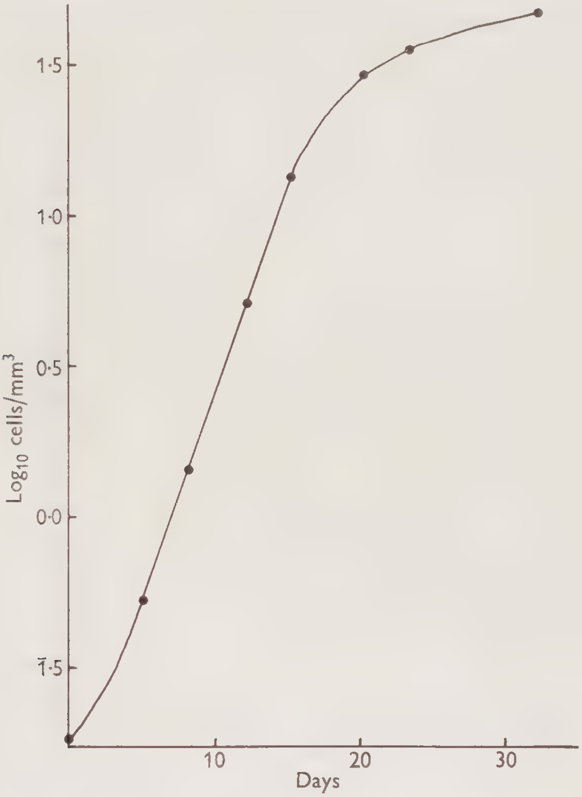

Fig. 1. The mean growth curve of three bacteria-free cultures of *Prorocentrum*.

Phosphorus supply

A similar experiment, also with bacteria-free cultures, was carried out in a series of concentrations of dipotassium hydrogen phosphate in medium BD and cell counts made after 29 days. The results are shown in Fig. 3.

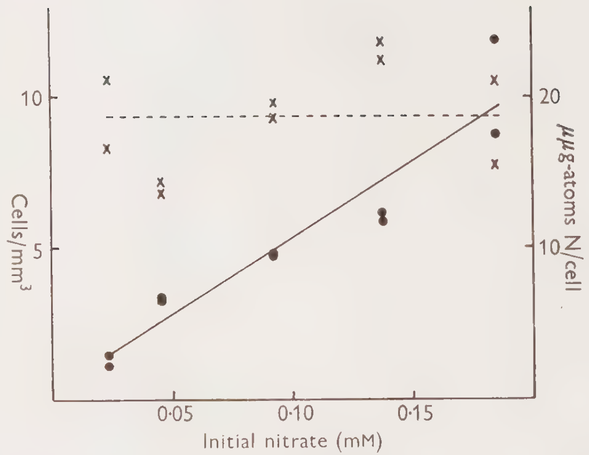

Fig. 2. The cell crop and nitrogen per cell of *Prorocentrum* in relation to concentration of potassium nitrate. –●—●–, cell crop; - × - - - × -, nitrogen/cell.

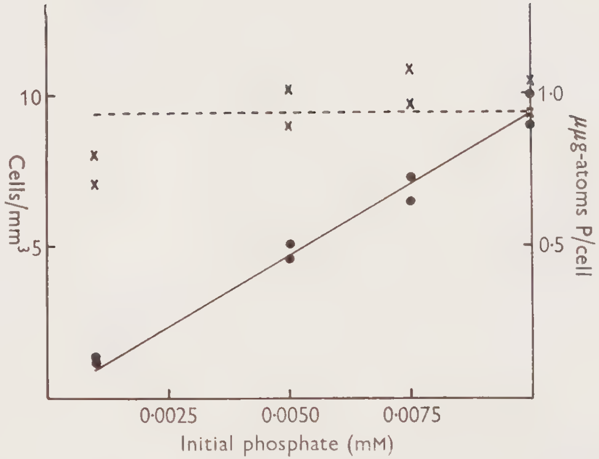

Fig. 3. The cell crop and phosphorus per cell of *Prorocentrum* in relation to concentration of dipotassium hydrogen phosphate. –●—●–, cell crop; - × - - - × -, phosphorus/cell.

Phosphorus was evidently limiting in all but the highest concentration and the mean requirement was 0·94 $\mu\mu$g-atom P/cell.

Trace elements

In experiments carried out in Erdschreiber medium cell concentrations of the order of only 10–15 cells/mm^3 were obtained in uni-algal culture. It was found that this could be increased significantly by the addition of 0·01 mM $FeCl_3$. Later Provasoli's trace element mixture as used for *Asterionella* and *Isochrysis* (Kain & Fogg, 1958*a*, *b*) was added to natural sea water enriched with the usual nitrate, phosphate and cobalamin concentrations and 50 ml./l. of soil extract. Ethylenediamine tetra-acetic acid (EDTA) was added at 0·171 and 0·342 mM. The final cell concentrations of the uni-algal culture in the latter (23·3, 23·9 and 27·8 cells/mm^3) were significantly greater than in the former (18·5, 19·4 and 14·7 cells/mm^3), with less EDTA. Medium AQ, which incorporates these concentrations of trace elements and EDTA at 0·342 mM, is therefore suitable for *Prorocentrum*.

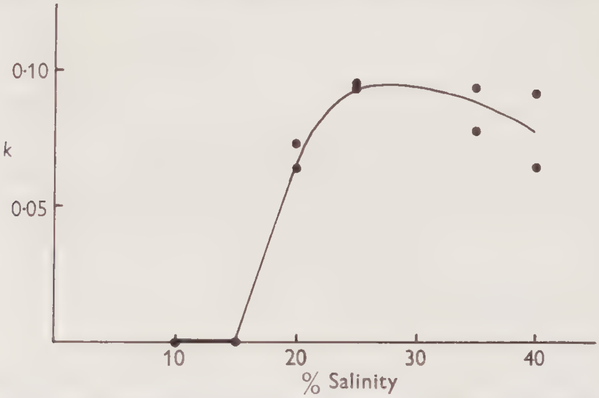

Fig. 4. The relative growth constant of *Prorocentrum* in media based on sea water of various salinities.

Salinity

The uni-algal culture of *Prorocentrum* was grown in medium AK based on sea water of various salinities. All the cultures were inoculated with cells from 35‰ salinity. The relative growth constants are shown plotted against salinity in Fig. 4. A range of 20–40‰ salinity was tolerated.

Artificial sea water

Experiments with artificial sea water gave irregular results. When it was compared directly in medium AQ_A with natural sea water in AQ_N, with cobalamin and soil extract added to both, growth took place in all the cultures, but after 46 days the cell concentrations were significantly lower in artificial sea water (2·54, 2·24 and 2·08 cells/mm^3) than in natural sea water (3·06, 2·70 and 3·24 cells/mm^3). On the other hand in the experiments on hydrogen-ion concentration, in which artificial sea water was used with soil extract, the relative growth constant was as high as has been observed (k = 0·38). Also the experiment to determine which of the twelve vitamins was necessary (see page 43) was based on artificial sea water without soil extract and the relative growth constant was normal, from a washed inoculum. Thus there is nothing unsuitable about the substances present in the artificial sea water though a medium made up from it may lack some stimulatory factor present in variable amounts in natural sea water. That this latter is the case with *Prorocentrum* as well as with *Asterionella* (see Kain & Fogg, 1958*a*) was strongly indicated by a further vitamin experiment with entirely synthetic media (BE_A) in which growth was very poor and irregular, though normal in control cultures in natural sea water (BE_N).

TABLE 2. THE RELATIVE GROWTH CONSTANTS OF *PROROCENTRUM* IN MEDIA AT DIFFERENT pH'S

pH:	7·5	7·75	8·0	8·25	8·5	8·75
k:	0·294	0·323	0·324	0·167	0·084	0·244
	0·304	0·322	0·316	0·322	0·355	0·379

Hydrogen-ion concentration

Bacteria-free *Prorocentrum* was grown in medium AQ_A with soil extract, cobalamin, vitamins S 3 and 16·5 mM tris. Various pH values were maintained by adjustments before and after autoclaving and after 5 days growth. The relative growth constants, calculated from cell counts made after 7 days, are shown in Table 2. The variable results above pH 8 were probably due to differences in precipitation during autoclaving. Apart from this there was no apparent effect between pH 7·5 and 8·75.

Light

In the course of an experiment on *Prorocentrum* it was noted that identical cultures in separate tanks at the same temperature illuminated by fluorescent and incandescent lamps, respectively, showed markedly different growths. Those in incandescent light flourished while those in fluorescent light ceased growth after two divisions. In investigating the optimum light intensity for this organism therefore, both types of lamp were used. As the spectral composition of light from the two types is different, the energy output per unit of illumination (e.g. lux) is not the same from each. It is therefore necessary to use energy units in direct comparisons.

In two experiments at relatively low light intensities the lag time was measured by extrapolating the exponential growth line back to the inoculum level. The results of this are shown in Fig. 5*a* (in incandescent light) and Fig. 5*b* (in fluorescent light, not inhibitory on this occasion). In both there was a reduction of lag with increasing light intensity, at least up to the saturation level.

Four experiments were made with incandescent light, using lamps of different wattages, with cultures at various distances from the source. The results are combined in Fig. 6*a*. The saturation level (at 20° C) was at about 300 μg-cal/cm^2 sec (or 3000 lux as indicated by a selenium photocell light metre). There was no inhibition at 3900 μg-cal/cm^2 sec (or 39,000 lux), an intensity which was obtained at about 10 cm from a 1000 W bulb.

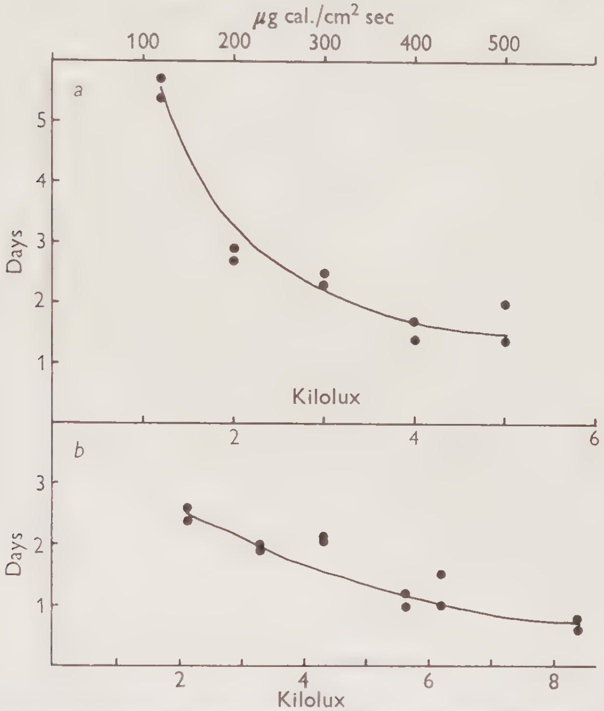

Fig. 5. The lag time of cultures of *Prorocentrum* in relation to light intensity. (*a*) From tungsten lamps. (*b*) From 'white' fluorescent tubes. The energy scale at the top applies to both (*a*) and (*b*).

The fluorescent tubes used were 'white'. The inhibition of growth by this type of light was observed in four separate experiments, involving two different makes of lamp, with identical control cultures in incandescent illumination in which growth was normal. The relative growth constants of some of these are shown as crosses in Fig. 6*b*. Below 150 μg-cal/cm^2 sec the growth constant increased with light energy but above this value it declined markedly.

In one experiment (shown as circles in Fig. 6*b*) over the same range of energy no inhibition was observed at all, and the relative growth constant increased with light energy to saturation at about 400 μg-cal/cm^2 sec. That the saturation energy was higher than that for incandescent light may be attributed to the less suitable spectral distribution of energy in fluorescent light or, since the relative growth rate achieved was higher in the latter, to the removal of some other limiting factor. It is not known what factors cause the inhibition by this type of light. The possibilities include the medium, the physiological state of the cells and the age of the fluorescent tubes.

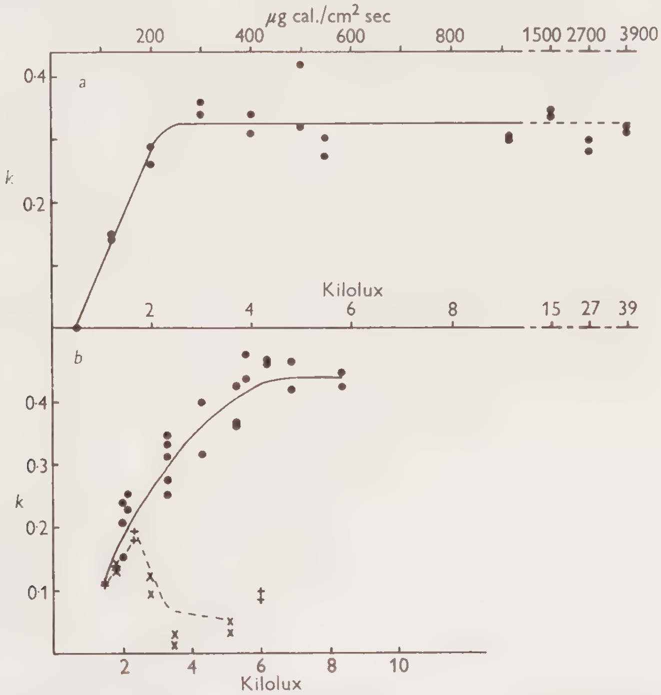

Fig. 6. The relative growth constant of *Prorocentrum* in relation to light intensity. (*a*) From tungsten lamps. (*b*) From 'white' fluorescent tubes. ●——, non-inhibitory; × +---, inhibitory.

In investigating the cause of the inhibition it is necessary to compare the emission spectrum of this type of fluorescent lamp with that of an incandescent tungsten filament bulb. These are shown in Fig. 7*a*, where the total relative energy, represented by the area below the curves, has been made the same between 380 and 720 mμ. The position of the principal peak in emission in the region of least absorption by *Prorocentrum* (Fig. 7*b*) indicates the unsuitability of this type of light for photosynthesis. It is possible that the wave-band 425–445 mμ could contain sufficiently more energy in fluorescent than incandescent light to account for the inhibition. The other possibility is that the ratio of wavelengths is in some way responsible. In this connexion it is worthy of note that the action spectrum of phototaxis of *P. micans* was found by Halldal (1958) to have its peak at about 575 mμ (see Fig. 7*b*), very near to the peak in emission of 'white' fluorescent light.

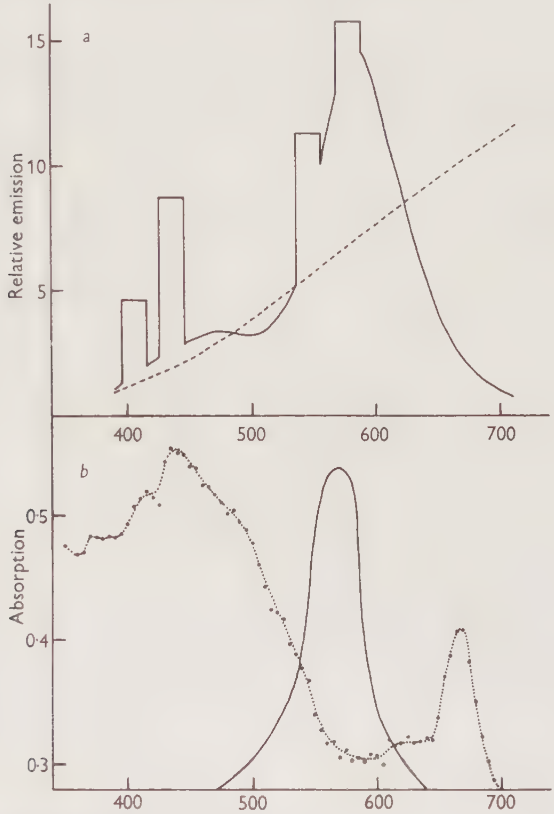

Fig. 7. (*a*) The emission spectra of lamps giving equal energy between 380 and 720 mμ. —, Ekco 'white' fluorescent tubes (by permission of Ekco-Ensign Electric Ltd.); - - -, tungsten filament lamp. (*b*) —, the phototaxis action spectrum of *Prorocentrum micans* (from Halldal, 1958); ···●···, the absorption spectrum of *P. micans* suspended in glycerol.

Stimulatory substances

In our early experiments on *Prorocentrum* in Erdschreiber medium it was found that soil extract was essential for good growth, especially when the culture was bacteria-free. In attempts to characterize the stimulatory factor a number of substitutes were tried. In all these experiments a mixture of twelve vitamins (see Table 1) in addition to nitrate, phosphate and iron was included in the basal sea-water medium. The results, expressed in terms of relative growth constants and in one case as the cell concentration at the end of the experiment, are shown in Table 3. It is clear that even in the presence of the vitamins soil extract was still stimulatory. Its action cannot be attributed to its providing any of these particular substances and the likely possibilities are that it was acting as a buffer or a chelator. The effect of its addition was therefore compared with that of the buffer tris, the chelator EDTA (with trace element additions) and glycylglycine, used by Droop (1958). The relative growth constant was found to be about the same in soil extract, tris and glycylglycine (Expt. 1, Table 3). With tris, however, the final cell populations attained were lower than in those media without this addition. With glycylglycine growth was almost as good as with soil extract throughout. In Expt. 2 (Table 3) glycylglycine clearly promoted faster growth than EDTA both by itself and when it was added together with the latter. The three most likely possibilities for the cause of the stimulation by glycylglycine are:

TABLE 3. RELATIVE GROWTH CONSTANTS OF *PROROCENTRUM* IN MEDIA (SEE TEXT) WITH VARIOUS ADDITIONS

Expt.	None	Soil extract	Tris	EDTA	Glycylglycine	Glycylglycine and EDTA
1*	0·234	0·309	0·287	—	0·304	—
	(23·4)	(80·5)	(27·1)	—	(46·8)	—
	—	0·295	0·304	—	0·292	—
	—	(62·2)	(27·3)	—	(58·5)	—
2	0·222	0·347	—	0·276	0·351	0·391
	0·135	0·337	—	0·244	0·322	0·369
3	—	—	—	0·305	—	0·402
	—	—	—	0·302	—	0·365
	—	—	—	—	—	0·350

* The figures in brackets are the cell concentrations after 26 days.

(1) As a buffer it acts during autoclaving in preventing the precipitation of essential ions.

(2) Again as a buffer it acts during the growth of the organism, reducing inhibitory pH changes.

(3) As a chelator it prevents the precipitation of essential ions or reduces the concentration of toxic ions.

If the first were the case then its superiority over EDTA would disappear if the autoclaving process were omitted. However, in Seitz-filtered media which were not autoclaved, the stimulation was still significant. In Expt. 3 (Table 3) the initial pH of the medium in both cases was about 6·4 and the final pH with EDTA alone was 8·2 while with glycylglycine it was 7·7 As the initial pH was the same and the final values both within the optimum range for the organism (Table 2) it is unlikely that the buffering action of glycylglycine is important in the stimulatory effect. It seems probable that it acts as a chelator, being in some way more suitable than either tris or EDTA.

Vitamins

Droop (1957) has already reported the requirement for cobalamin of the organism. In order to determine which of the twelve vitamins used in the current media were necessary, thirteen duplicate cultures were grown in medium BE_A, in each one of twelve of which a different vitamin was omitted. The inoculum was washed and the concentration of the previous medium was 0·06%. Cotton-wool plugs were not used. The cell concentrations after 11 and 18 days are shown in Table 4. The requirement for cobalamin was confirmed by the low and stationary (after 11 days) cell concentration in its absence. Growth was also less in the absence of biotin. None of the other vitamins appear to have been necessary, though it is doubtful whether a single experiment, even using a washed inoculum, is sufficient to establish the independence of the organism from external sources of these substances.

TABLE 4. THE CELL CONCENTRATIONS IN CULTURES WITH VITAMIN OMISSIONS

(Cells/mm^3)

	11 days		18 days	
No omission (i.e. with twelve vitamins)	13·8	13·4	32·9	34·2
No thiamin	16·1	13·5	33·3	27·6
No riboflavine	15·9	14·0	31·2	24·9
No pantothenic acid	14·3	6·46	24·0	15·9
No nicotinic acid	12·8	9·44	25·7	23·8
No pyridoxine	11·6	12·7	23·6	30·7
No cobalamin	2·68	3·08	3·14	3·00
No *p*-amino benzoic acid	14·7	12·4	28·9	29·7
No inositol	14·3	12·8	27·8	32·3
No biotin	7·95	7·69	12·0	9·67
No folic acid	15·9	12·6	31·4	28·2
No adenine	17·2	11·4	30·8	31·0
No guanine	11·7	15·5	27·8	27·4

DISCUSSION

These results obtained with *Prorocentrum micans* will now be considered, together with those presented in previous papers of the series (Kain & Fogg, 1958*a*, *b*) for *Asterionella japonica* and *Isochrysis galbana*.

Nitrogen supply

Nitrate has been the only source of nitrogen used in our work but appears to be the most generally suitable source for phytoplankton. In common with workers studying various other kinds of algae (see Fogg, 1959) we have been unable to demonstrate the limitation of exponential growth rate by nitrate concentration. Barker (1935) had already shown that the exponential growth of *Prorocentrum micans* is unaffected by variation in nitrate concentration between 0·016 and 16 mM. At limiting concentrations, the final yield of cell material is proportional to the amount of nitrate originally supplied (Spencer, 1954; Miller & Fogg, 1957) and a minimum nitrogen content per cell is approached. From our results it is possible to determine the minimum nitrogen requirement per cell which is not necessarily equivalent to minimum nitrogen content per cell, since a proportion of the nitrogen assimilated may be liberated in extracellular form. Some values for the minimum nitrogen content or requirement per cell are given in Table 5. From approximate cell volumes determined from models, values for the mean nitrogen content per unit volume of protoplast have been calculated and are seen to be of the same order for the various organisms considered. Above the minimum value the nitrogen content per cell may vary greatly and it is to be expected that such variations are accompanied by considerable changes in metabolic activity and pattern (Fogg, 1959).

TABLE 5. MINIMUM NITROGEN CONTENT OR REQUIREMENT PER CELL OF VARIOUS ALGAE

Species	Cell volume μ^3	$\mu\mu$g-atoms N/cell	μg-atoms N/mm^3	Author
Asterionella japonica	920	0·25	0·27	Kain & Fogg, 1958*a*
A. formosa	1,800	0·4	0·4	Lund, 1950
Isochrysis galbana	31	0·051	1·6	Kain & Fogg, 1958*b*
Prorocentrum micans	17,000	19	1·1	This paper
Peridinium I	3,200	1·5	0·47	Barker, 1935
Monodus subterraneus	120	0·0228	0·19	Miller & Fogg, 1957

Phosphorus supply

Orthophosphate has been the only source of phosphorus used in our experiments and, as for nitrate, it is difficult to determine the concentrations which would limit the exponential growth rate. Ketchum (1939*b*) reported that variation in phosphate concentration between 0·00053 and 0·0016 mM had no effect on the relative growth constant of *Nitzschia closterium*. The growth of some algae is inhibited by high phosphate concentrations of the order of 0·5 mM (Chu, 1943; Provasoli & Howell, 1952). For *Asterionella japonica* we have found that the relative growth rate remains constant within the range 0·01 to 0·31 mM phosphate. The phosphorus content of algal cells may vary within wide limits according to conditions, but for a given species the minimum content is fairly constant (Ketchum, 1939*a*; Goldberg, Walker & Whisenand, 1951; Mackereth, 1953). Values for the minimum phosphorus requirement of various algae, determined as for minimum nitrogen requirements, are given in Table 6, from which it seems that, while the mean phosphorus requirement or content per unit volume of protoplasm may be fairly constant for the marine species, those for freshwater species may be an order of magnitude lower.

Salinity

Of the three organisms studied, *A. japonica* is the least tolerant of variations in salinity, having a well-defined optimum in relative growth rate between 30 and 35‰ salinity. In contrast, the relative growth rate of *Isochrysis galbana* is little affected by variation between 15 and 40‰ salinity. The results obtained for *Prorocentrum micans* (optimum between 25 and 40‰ salinity) are in reasonable agreement with those of Braarud & Rossavik (1951).

TABLE 6. MINIMUM PHOSPHORUS CONTENT OR REQUIREMENT PER CELL OF VARIOUS ALGAE

Species	Cell volume (μ^3)	μμg-atoms P/cell	μg-atoms P/mm^3	Author
Asterionella japonica	920	0·05	0·05	Goldberg *et al.*, 1951
Nitzschia closterium	580	0·0066	0·011	Ketchum, 1939*a*
Asterionella formosa	1,800	0·0018	0·001	Rodhe, 1948
	—	0·0006	0·0003	Lund, 1950
	—	0·002	0·001	Mackereth, 1953
Isochrysis galbana	31	0·00097	0·03	Kain & Fogg, 1958*b*
Prorocentrum micans	17,000	0·94	0·055	This paper
Peridinium I	3,200	0·159	0·05	Barker, 1935
Monodus subterraneus	120	0·00089	0·007	Miller & Fogg, 1957

Temperature

Previous determinations of the effects of temperature on phytoplankton organisms (Barker, 1935; Ryther, 1954; Spencer, 1954; Nordli, 1957) have shown the lower and upper limits for growth to be about 5° and 30° C and the optima to be usually between 15° and 27° C. The precise values obtained in a given experiment will vary according to conditions, e.g. light intensity and the presence of bacterial contaminants may have important effects. Our results are in general agreement with those of previous workers and it seems that the optimum temperatures for the growth of the three species studied are higher than any they are likely to encounter in nature.

Light intensity

The comparison of results obtained by different workers on the effect of light intensity on algal growth is difficult. Two sets of units (of illuminance and of irradiance), which are not readily interconvertible, are in use; the geometry of the apparatus used and the density of the suspension may have effects making the actual light intensity reaching the cells considerably different from that recorded by a photometer; and the calibration of commercial photometers cannot be relied upon (Myers, 1946). Determinations of effects on photosynthesis cannot be taken as being equivalent to the effects on growth since saturating intensities for the former may be much higher than for the latter (Myers, 1951). Our determinations of the effect on growth gave values which are of the same order as those found in other studies on algae. The saturating intensity for *Asterionella japonica*, *c.* 4000 lux from a tungsten lamp (400 μg-cal/cm^2 sec) is about the same as those reported for various fresh-water *Chlorella* species, a *Scenedesmus* and a *Chlamydomonas* (Sorokin & Krauss, 1958). That for *Isochrysis galbana* is lower, *c.* 1500 lux (150 μg-cal/cm^2 sec), but similar values have been recorded for *Chlorella pyrenoidosa* (Myers, 1953). The relative growth rate of *Prorocentrum micans* reaches its maximum at 300–400 μg-cal/cm^2 sec. We have not observed light inhibition of the growth of either *Asterionella japonica* or *Isochrysis galbana*; the highest light intensities used being well below 20,000 lux, at which intensity inhibitory effects on the growth of Chlorophyceae become apparent (Sorokin & Krauss, 1958). No inhibition of the growth of *Prorocentrum micans* was found by us in light of an intensity of 39,000 lux (3900 μg-cal/cm^2 sec) from tungsten lamps. On a number of occasions, though not invariably, we have observed inhibition at 3000 lux (200 μg-cal/cm^2 sec) from 'white' fluorescent tubes. Nordli (1957) has also recorded inhibition of the growth of dinoflagellates by relatively low intensities of light from fluorescent lamps but Haxo & Sweeney (1955), who used light from 'white' fluorescent tubes, found 5000–8000 lux to be optimal for *Gonyaulax polyedra* and made no mention of inhibitory effects. Nordli (1957) attributed the more marked inhibition of *Ceratium furca* by continuous light from fluorescent lamps to the overstimulation of phototaxis, but further work is needed to establish this point.

Hydrogen-ion concentration

Until buffers such as tris(hydroxymethyl)aminomethane were used (Provasoli, McLaughlin & Pintner, 1954) there was difficulty in controlling the pH of sea-water media and information on the effect of pH on the growth of marine phytoplankton is correspondingly scanty. Our results support the conclusion of Bachrach & Lucciardi (1932) that the pH optimum for marine diatoms is near to that of natural sea water. The lower limit of the optimum range is less than pH 7·5 for the three organisms studied by us. *Asterionella japonica* seems to be the most sensitive to alkaline conditions, an appreciable decrease in relative growth constant occurring above pH 8·25, while *Prorocentrum micans* is the most tolerant, the maximum relative growth constant being maintained to at least pH 8·75. Our results for *P. micans* are in good agreement with those obtained previously for this organism by Barker (1935).

Other factors affecting growth

Requirements for organic substances have now been established for many marine phytoplanktonic organisms (see the reviews by Droop, 1957 and by

Provasoli, 1957, 1958*a*, *b*). Our failure to grow *Asterionella japonica* in the absence of bacteria and other pieces of evidence suggest that this organism has a requirement for one or more organic growth factors and there are also indications that it produces an autoinhibitor in the course of growth. The chemical nature of these substances is as yet entirely unknown. *Prorocentrum micans*, isolated by us into bacteria-free culture, appears to require cobalamin and biotin in addition to some other possible substance. Since our work was completed it has been reported that *Isochrysis galbana* has requirements for cobalamin and thiamin (Provasoli, 1958*b*).

THE LARGE-SCALE CULTURE OF MARINE PHYTOPLANKTON

The mass culture of microscopic algae is a possible means of producing feedingstuffs or organic materials for industry. While the use of sea water rather than fresh water as a medium for this has no intrinsic value it might be more economic in certain circumstances. The general principles underlying the large-scale culture of algae have been considered in several publications (e.g. Tamiya, 1957; Thacker & Babcock, 1957; Fogg, 1957) and here it is our intention only to comment briefly on such features of the organisms studied by us as seem important for their growth in large-scale cultures.

TABLE 7. GROWTH CHARACTERISTICS OF SOME UNICELLULAR MARINE ALGAE AND OF *CHLORELLA PYRENOIDOSA*

Species	Author	Conditions	Relative growth constant ($\log_e$ units/day)	Final cells/ml
Phaeodactylum tricornutum	Spencer, 1954	Laboratory culture	1·7 (25° C)	—
	Raymont & Adams, 1958	Large-scale tanks	0·69 (13·5°—18° C)	$3{\cdot}2 \times 10^7$
Chlorella sp. (marine)	Loosanoff, 1951	Large-scale tanks	—	$3{\cdot}5 \times 10^7$
Dunaliella bioculata	Eddy, 1956	Laboratory culture	1·1 (25° C) 1·8 (29° C) 2·9 (33·5° C)	$2{\cdot}5 \times 10^7$ $1{\cdot}2 \times 10^7$ $7{\cdot}2 \times 10^6$
Asterionella japonica	Kain & Fogg, 1958*a*	Laboratory culture	1·2 (20–25° C)	$4{\cdot}0 \times 10^6$
Isochrysis galbana	Kain & Fogg, 1958*b*	Laboratory culture	0·55 (20° C)	$2{\cdot}4 \times 10^7$
Prorocentrum micans	This paper	Laboratory culture	0·3 (20° C)	$5{\cdot}0 \times 10^4$
Chlorella pyrenoidosa	Thacker & Babcock, 1957	Large-scale continuous aseptic culture	2·0 (25° C)	$3{\cdot}7 \times 10^8$

The maximum relative growth rates of *Asterionella japonica*, *Isochrysis galbana* and *Prorocentrum micans* are lower than those of other organisms which have been considered from this point of view (Table 7), but this is not necessarily of great importance since in mass culture the aim should be to achieve a linear phase of growth in which yield per unit time is proportional to the amount of light received. Here, there may be an advantage in using organisms such as *Asterionella japonica* and *Prorocentrum micans* which require relatively high intensities for saturation and which may thus give greater yields for a given amount of light. The maximum yield per unit volume of medium is of considerable importance for successful large-scale culture, since dense suspensions are necessary for economic handling. The maximum final cell concentration achieved in cultures of marine algae have so far been only about one-tenth of those achieved in ordinary large-scale cultures of *Chlorella* (Table 7) and even when differences in cell size are allowed for the yield per unit volume of the former remains poor by comparison. In our densest cultures nitrate, phosphate, salinity, hydrogen-ion concentration and carbon dioxide were not limiting and the nature of the factors determining the final population density is unknown; natural sea water with simple additions of nitrate and phosphate is not necessarily the medium giving maximum yields of these organisms and it may be that adjustment of ionic ratios, as has proved successful with the freshwater alga *Monodus* (Miller & Fogg, 1957), or addition or removal of organic factors will be necessary to obtain worthwhile improvements in yield. Finally, it may be pointed out that harvesting is one of the most expensive processes in the mass culture of algae and that organisms such as *Asterionella japonica* and *Prorocentrum micans*, being considerably larger, are more readily separated from the culture medium than is *Chlorella*.

Part of this work was carried out under extra-mural contract with the Institute of Seaweed Research. We are grateful to the Institute for a maintenance grant made to one of us (J. M. K.). We are also very grateful for the technical assistance of Miss W. B. Chapman.

SUMMARY

The dinoflagellate *Prorocentrum micans* has been grown in bacteria-free, as well as uni-algal, culture under controlled conditions and its growth measured by means of cell counts.

The relative growth constant was about 0·3 $\log_e$ units/day. Ranges of salinity of 20–40‰ and of pH of 7·5–8·75 were tolerated. The optimum incandescent light intensity was 3000–39,000 lux (300–3900 μg-cal/cm^2 sec). Fluorescent light of more than 2000 lux (150 μg-cal/cm^2 sec) was usually inhibitory, a phenomenon which may have been associated with phototaxis. The lag time decreased with increasing light intensity.

The provision of a suitable chelator seemed very important for this organism. Ethylenediamine tetra-acetic acid was fairly satifactory but glycylglycine was better. Its requirement for cobalamin was confirmed and it was also found to need biotin. Prolonged growth in a completely synthetic medium was not achieved.

A final cell concentration of 50–80 cells/mm^3 was obtained. The minimum nitrogen requirement was 19 $\mu\mu$g-atoms N/cell and the minimum phosphorus requirement 0·94 $\mu\mu$g-atoms P/cell.

The results from the three organisms studied in this series are compared with those obtained by other workers.

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STEROID SULPHATASE, ARYLSULPHATASE AND β-GLUCURONIDASE IN MARINE INVERTEBRATES

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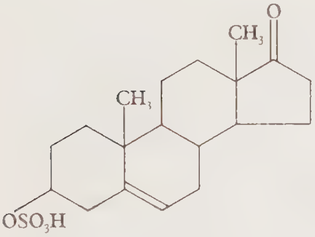
The widespread occurrence of sulphatases in the Mollusca was first demonstrated by Soda & Hattori (1933*a*, *b*) who showed that these enzymes are mainly concentrated in the digestive glands. That extracts from marine molluscs also possess β-glucuronidase activity was first noted by Dodgson, Lewis & Spencer (1952) who studied the optimum conditions for the activity of this enzyme and arylsulphatase in *Patella vulgata* (L.) and *Littorina littorea* (L.) and applied their findings in an investigation of the distribution of both enzymes among various other marine molluscs (Dodgson, Lewis & Spencer, 1953).

Molluscan tissues have also been investigated as a possible source of a sulphatase capable of hydrolysing the steroid conjugates normally encountered in human urine (Henry & Thevenet, 1952; Stitch & Halkerston, 1953*a*, *b*; 1956; Jayle & Baulieu, 1954; Savard, Bagnoli & Dorfman, 1954; Roy, 1954, 1956*a*; Leon, Bulbrook & Corner, 1960). The main reason for such studies has been the need to find an alternative to acid hydrolysis of the steroid conjugates, a method which causes much destruction and alteration of some of the liberated steroids. However, although many of the gastropods studied possess an enzyme capable of hydrolysing dehydro*epi*androsterone sulphate (I), and some species belonging to this class possess an enzyme which will also hydrolyse aetiocholanolone sulphate (II), it has not been possible to detect an enzyme which would effect the hydrolysis of androsterone sulphate (III). This means that complete enzymic hydrolysis of all the steroid conjugates present in human urine cannot be achieved with any of the molluscan enzymes studied so far. Moreover, sulphatases from other sources, such as mammalian liver (Gibian & Bratfisch, 1956; Roy, 1957), fungi (Cohen & Bates, 1949; Stitch & Halkerston, 1953*b*), and bacteria (Buehler, Katzman & Doisy, 1950) have also proved to be unsuitable for this purpose.

The present work is an extension of an earlier study (Leon *et al.*, 1960) in which a search was made for a convenient source of a 'steroid sulphatase' that would effect the hydrolysis of androsterone sulphate. In this paper the term 'steroid sulphatase' is used to describe any enzyme which will effect the hydrolysis of a steroid sulphate. However, since the role of these enzymes in mammalian and molluscan tissues is not known, the use of this term is not intended to imply physiological function. In the earlier investigation all the animals used belonged to the mollusca, but in the present study species representative of eight additional marine invertebrate phyla have been examined, and the activities of arylsulphatase and β-glucuronidase in these animals have been examined in relation to their diets, habitats and methods of feeding. No steroid sulphatase has been detected in any marine animal tested other than certain molluscs of the class gastropoda, and there appears to be no correlation between the activity of this enzyme and the diet of the animal in which it is present. Moreover, even the most active preparations of steroid sulphatase so far studied have no measurable influence on the hydrolysis of androsterone sulphate, and an enzyme capable of effecting this change has therefore still to be found.



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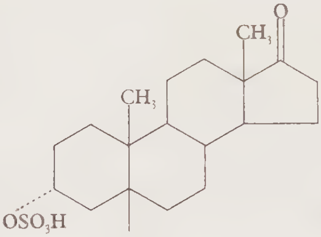

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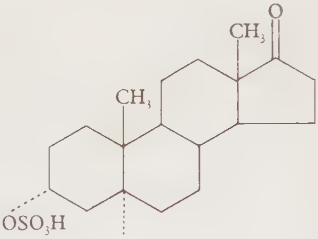

III

MATERIALS AND METHODS

Animals. Test species were collected from the intertidal zone or from the off-shore waters in the vicinity of Plymouth, with the exception of *Helix pomatia* L., specimens of which were gathered in a Sussex garden. This terrestrial species was included for comparison because enzyme preparations from *Helix* have been used for the hydrolysis of steroid conjugates. Full names of all the test species are given in Tables 1 and 2, but are not hereafter used in any part of the text other than the summary.

Extraction of enzymes. Acetone-dried powders were prepared from the tissues of approximately twenty animals of each test species. Exceptions to this were *Marinogammarus*, *Ligia* and *Procerodes* where much larger numbers of test animals were used; and *Maia*, *Cancer*, *Clionacelata*, *Ciona* and *Sepia* where the number of test animals was only two or three. Whenever possible the digestive gland was the tissue used in preparing the enzymes, but in many instances dissection of this organ was prohibited by the smallness of the test species, and the whole animal was then used.

Estimations of enzyme activity. Arylsulphatase was assayed using dipotassium 2-hydroxy-5-nitrophenylsulphate (NCS) and potassium nitrophenylsulphate (NPS) as substrates; the method employed was that described by Dodgson *et al.* (1953).

Androsterone, dehydro*epi*androsterone and aetiocholanolone sulphates (AS, DHAS and AeS respectively), were used in estimations of steroid sulphatase activity by the method of Roy (1956*a*, *b*). β-Glucuronidase was assayed by the method of Dodgson *et al.* (1953), using *p*-chlorophenylglucuronide monohydrate as the substrate.

RESULTS

β-Glucuronidase and arylsulphatase

The experimental findings, summarized in Tables 1 (Mollusca) and 2 (other phyla), demonstrate the widespread occurrence of β-glucuronidase and arylsulphatase among marine invertebrates. Thus, each of the twenty-three species tested was found to possess some arylsulphatase activity, although two species with low activity towards NCS (*Ligia* and *Antedon*) were inactive when NPS was used as substrate. β-Glucuronidase activity was found in eighteen of the species tested, but was not detected in *Turritella* (Mollusca), *Marinogammarus* and *Ligia* (Arthropoda), *Clionacelata* (Porifera) and *Amphioxus* (Cephalochorda).

The number of species used in experiments with molluscs was sufficient to allow examination of the possibility of a correlation between enzyme activity on the one hand and diet and habitat on the other (Table 3). The figures in the first row of the table include all the species of molluscs tested and show that β-glucuronidase activity is much greater in the herbivorous than in the carnivorous or detritus-eating species. There is a similar but less marked difference in the mean values for arylsulphatase activity. These figures include the results obtained using acetone-dried powders prepared from two herbivorous and two detritus-eating species where the whole animal was used. If the enzymes are mainly concentrated in the digestive gland then only the results of experiments in which these glands were used are strictly comparable. The figures in the second row of the table are derived from the results on species where it was possible to dissect out the digestive glands, and they emphasize the difference in β-glucuronidase levels between the herbivorous, the carnivorous, and the detritus-eating species. The figures show again the raised arylsulphatase levels in the herbivores compared with the carnivores but the mean value for the arylsulphatase of the detritus-eating species is not significantly different from that of the herbivores. It is worth mentioning that the differences between the enzyme activities of herbivorous and carnivorous molluscs would be even greater were it not for the anomalous result obtained using *Nassarius*, which possesses a very high arylsulphatase and β-glucuronidase activity, but is described as carnivorous (see Table 1). However, although the animal is reported to feed largely on carrion, there is a possibility that it may inadvertently ingest a certain amount of plant material as well, and so, to some extent, be omnivorous (A. Graham, private communication).

TABLE 1. β-GLUCURONIDASE AND ARYLSULPHATASE ACTIVITY IN MOLLUSCS

Species	Test material		Source of enzyme	Enzyme activities*		
				Arylsulphatase		β-Glucuronidase
	Habitat	Feeding and diet		NCS	NPS	
Patella vulgata (L.)	Intertidal	Browses on algal sporelings and diatoms (1)	Visceral hump	652,335	157,450	155,900
Littorina littorea (L.)		Browses on algal sporelings and diatoms (1) (3)	Whole animal without shell	585,860	168,920	69,070
Lepidochitona cinerea (L.)		Diatoms and algal detritus (1)	Whole animal	41,200	25,220	10,890
Patina pellucida (L.)		*Laminaria* and attached sporelings and diatoms (1) (2)	Whole animal	25,620	7,450	23,790
Aplysia punctata (Cuvier)		*Ulva*, *Fucus* (1) (4)	Digestive gland	287,390	55,030	28,520
Nucella lapillus (L.)		Carnivorous (barnacles and mussels) (1)	Digestive gland	96,260	39,550	15,480
Nassarius reticulatus (L.)	Offshore; mud deposits	Carnivorous (barnacles and mussels (1)	Digestive gland	435,930	235,610	75,800
Buccinum undatum L.	Offshore; gravel and mud deposits	Carnivorous (crabs, worms, etc.) (1)	Digestive gland	227,830	81,400	14,620
Turritella communis (Risso)		Ciliary feeder on detritus (7)	Whole animal	181,440	37,070	0
Crepidula fornicata (L.)		Ciliary feeder on detritus (1) (5)	Digestive gland	74,100	9,360	8,310
Pecten maximus (L.)		Ciliary feeder on detritus (6)	Digestive gland	941,110	449,050	16,910
Sepia officinalis (L.)	Pelagic	Carnivorous (*Crangon*, etc.)	Digestive gland	58,860	19,490	9,740
Helix pomatia (L.)	Terrestrial	Herbivorous (green plants)	Digestive gland	759,670	367,260	230,700
			Crop fluid	2,551,170	823,190	58,460

Arylsulphatase activity tested at pH 5·5; β-glucuronidase activity at pH 4·0; Activities are expressed as μg. phenol liberated/g powder/h.
References: (1) Graham, 1955; (2) Graham & Fretter, 1947; (3) Graham (unpublished observations); (4) Eales, 1921; (5) Orton, 1912; (6) Hunt, 1925; (7) Yonge, 1947.

* These figures for enzymic activity have been previously reported by Leon *et al.* (1960) and are reproduced here to show the correlation between enzyme activity and ecological data.

TABLE 2. β-GLUCURONIDASE AND ARYLSULPHATASE ACTIVITY IN ANIMALS OF PHYLA OTHER THAN MOLLUSCA

	Test material					Enzyme activities		
						Arylsulphatase		
Phylum	Class	Species	Habitat	Feeding and diet	Source of enzyme	NCS	NPS	β-Glucuronidase
Arthropoda	Malacostraca	*Cancer pagurus* L.	Intertidal	Carnivorous	Digestive gland	157,200	45,860	15,480
Arthropoda	Malacostraca	*Maia squinado* (Herbst)	Offshore; sandy or rocky localities	Carnivorous; also browses on algal tufts (1)	Digestive gland	280,460	77,580	7,450
Arthropoda	Malacostraca	*Marinogammarus marinus* (Leach)	Intertidal	Browses; chiefly vegetable detritus	Whole animal	38,780	9,940	0
Arthropoda	Malacostraca	*Ligia oceanica* (L.)	Intertidal	Browses; *Fucus* and small epiphytic algae on large sea weeds (3)	Whole animal	7,270	0	0
Coelenterata	Anthozoa	*Calliactis parasitica* (Couch)	Offshore; attached to shells inhabited by *Eupagurus*	Carnivorous	Whole animal	21,470	7,640	5,450
Echinodermata	Crinoidea	*Antedon bifida* (Pennant)	Offshore; mud deposits	Ciliary feeder; detritus and small living organisms	Whole animal	10,040	0	7,740
Porifera	Demospongiaria	*Clionacelata* (Grant)	Offshore; boring in rocks	Ciliary feeder; detritus and small living organisms	Whole animal	88,290	28,850	0
Platyhelminthes	Turbellaria	*Procerodes ulvae* (Oersted)	Intertidal	Browses; unicellular algae (2)	Whole animal	9,700	3,630	9,310
Tunicata*	Ascidiacea	*Ciona intestinalis* (L.)	Offshore; attached to submerged structures	Ciliary feeder; detritus (4)	Whole animal	—	—	—
Cephalochorda*	—	*Amphioxus lanceolatus* (Pallas)	Offshore; shell gravel	Ciliary feeder; detritus (5)	Digestive system	109,420	22,550	0
Annelida	Polychaeta	*Chaetopterus variopedatus* (Renier)	Offshore; muddy gravel	Ciliary feeder; detritus (6)	Whole animal	36,010	14,140	24,500

Experimental conditions as in Table 1.
References: (1) Carlisle (1957); (2) Spooner (unpublished observations); (3) Nicholls (1931); (4) MacGinitie (1939*b*); (5) Hunt (1925); (6) MacGinitie (1939*a*).

* Sub-phyla of the Chordata.

Although Dodgson *et al.* (1953) state that enzymic activity cannot be correlated with feeding habits, re-examination of their results shows the same trend as that in Table 3—namely, that the herbivorous molluscs have greater levels of β-glucuronidase and arylsulphatase activity than the carnivorous species.

Reference to both Tables 1 and 2 shows that of the eight species examined which are thought to feed on detritus, four were without β-glucuronidase-activity; whereas, of a further fourteen species which appear to be definitely carnivorous or herbivorous, only one (*Ligia*) was found to lack the enzyme. Correlation between habitat and enzyme activity merely reflects the fact that the herbivorous species are intertidal, whereas the carnivorous animals may, in addition, be pelagic or live off-shore in gravel or muddy deposits. Tables 1 and 2 show that many of the species that contain sulphatase and β-glucuronidase dwell on a substratum of muddy composition and the question arises of whether their enzymes are of bacterial origin, not being extracted from the tissues of the animals but from the bacterial flora that inhabit them. However, this does not seem likely, for Dodgson, Melville, Spencer & Williams (1954) have shown that the bacteria present in the digestive organs of certain marine molluscs have only a very low arylsulphatase activity; and it has been found in the present work that acetone-dried powders, prepared from samples of mud collected from the habitats of the various test animals, possessed only a slight enzymic activity, far less than would account for the activities of the preparations obtained using the tissues of the animals concerned.

'*Steroid sulphatase*'

'Steroid sulphatase' activity appears to be confined to the phylum mollusca; it was not detected in any of the other invertebrate phyla. It was only found in seven of the mollusca tested, each of these belonging to the subclass Prosobranchia of the class Gastropoda. Moreover, the enzyme was not found in all members of the Prosobranchia; and it was absent from the only species representing a different subclass of the gastropods, *Aplysia* from the Opisthobranchia (Table 4). The gastropods can be divided into two groups, according to the specificity of their steroid sulphatase. Thus, enzymes from four of the species tested would only effect the hydrolysis of DHAS, whereas enzymes from three species were active when both DHAS and AeS were used as substrates. In Table 4 the species are listed in order of maximum DHAS sulphatase activity, and it is of interest to note that the species with the highest activity are those which will also hydrolyse AeS. Two of these species belong to the carnivorous order, Stenoglossa; the third is the herbivorous land snail, *Helix*. It was not possible to detect an enzyme that would effect the hydrolysis of AS in any of the species tested. There is no apparent correlation between steroid sulphatase activity and diet and habitat because, of the marine molluscs that possess this enzyme, three are carnivores and three are herbivores.

TABLE 3. THE RELATIONSHIP BETWEEN ENZYMIC ACTIVITY AND FEEDING HABITS IN THE MOLLUSCA

The enzyme levels found for the digestive gland of *Helix pomatia* are included but not those found for the crop fluid.
The figures in the table are mean levels, calculated from the data in Table 1.
The figures in brackets in the columns headed NCS refer to the number of results from which the mean was derived. Units of enzyme activity are those defined under Table 1.

	NCS			NPS			β-Glucuronidase		
	Herbivores	Carnivores	Detritus	Herbivores	Carnivores	Detritus	Herbivores	Carnivores	Detritus
All preparations	462,175 (5)	204,720 (4)	309,463 (4)	151,222	94,013	130,175	101,596	29,810	9,027
Digestive gland preparations only	566,465 (3)	204,720 (4)	507,600 (2)	193,247	94,013	229,205	138,373	28,910	12,610

TABLE 4. STEROID SULPHATASE ACTIVITY OF VARIOUS MOLLUSCS

Activities are expressed as μg steroid liberated/g Powder A

Species	Order	Subclass	Class	Steroid sulphatase AeS	Steroid sulphatase DHAS
Nassarius reticulatus	Stenoglossa	Prosobranchia	Gastropoda	10,409	10,650
Helix pomatia	—	—		8,138	8,147
Buccinum undatum	Stenoglossa	Prosobranchia		12,056	3,592
Nucella lapillus	Stenoglossa			0	2,900
Patella vulgata	Archaeogastropoda			0	2,012
Patina pellucida	Archaeogastropoda			0	900
Littorina littorea	Mesogastropoda			0	891
Turritella communis	Mesogastropoda			0	0
Crepidula fornicata	Mesogastropoda			0	0
Aplysia punctata	Aplysiomorpha	Opisthobranchia		0	0
Pecten maximus	Pseudo-lamellibranchia	—	Lamellibranchia	0	0
Lepidochitona cinerea	—	—	Polyplacophora	0	0
Sepia officinalis	Decacera	—	Cephalopoda	0	0

The very active preparation of steroid sulphatase obtained from the digestive glands of *Nassarius* has been used in studies of the enzyme under different environmental conditions. The findings have shown that when DHAS is used as the substrate enzymic activity at 37° C. is four times as great as that at 12° C., and that when the test medium consists of 50% sea water, all enzymic activity disappears.

DISCUSSION

β-Glucuronidase and arylsulphatase

Vertebrates possess enzyme systems that effect the conjugation of phenolic substrates with sulphuric and glucuronic acids. Many phenolic substances, both of endogenous and exogenous origin, are excreted in the urine after conjugation as sulphates or glucuronides. In contrast, the physiological significance of β-glucuronidase, and various sulphatases which are concerned in the hydrolysis of glucuronic and sulphuric acid conjugates and are of widespread occurrence, has not yet been established. The possible function of these enzymes in the marine invertebrates is the hydrolysis of glucuronides and sulphates present in the diet. Thus, the finding that so many species of marine invertebrates possess arylsulphatase and a β-glucuronidase implies that these animals, although they show marked differences of phyla, habitat and method of feeding, must all live on diets containing sulphuric acid and glucuronic acids in conjugated form. These substances occur as structural units in certain polysaccharides and mucopolysaccharides. Thus, the hemicelluloses of plant origin contain glucuronic acid, and other polysaccharides such as hyaluronic acid and chondroitin sulphate, found in animal tissues, contain sulphuric acid as well. While the polysaccharide commonly found in marine plants (alginic acid) and animals (chitin) possesses uronic acids other than glucuronic as the structural unit, it is possible that polysaccharides other than alginic acid and chitin occur in the diets of marine animals. However, the exact substrates on which the invertebrate enzymes act are still unknown (Roy, 1956*a*).

The view that β-glucuronidase and arylsulphatase are involved in digestion is supported to some extent by the finding that, compared with carnivorous molluscs, herbivores possess a much higher enzyme activity; for it seems likely that this is because the latter species have to deal with a diet consisting of plants with thick cell walls.

'Steroid sulphatase'

Unlike arylsulphatase and β-glucuronidase, steroid sulphatase appears to have no obvious role as a digestive enzyme. The animals that possess it have very varied diets and feeding habits, which also closely resemble those of certain members of other classes and phyla from which the enzyme is absent.

The distribution of steroid sulphatase is interesting because the enzyme has been detected in only two classes in the ten phyla so far examined. These are the mammalia (Gibian & Bratfisch, 1956; Roy, 1957); and certain molluscs of the class Gastropoda, subclass Prosobranchia. Moreover, among marine gastropods, only those of the order Stenoglossa were found to possess an enzyme capable of hydrolysing AeS. However, the significance of the distribution of steroid sulphatase remains difficult to assess until a more comprehensive study has been made using a larger number of specimens from each phylum.

Preliminary results which show that a steroid sulphatase of use in the hydrolysis of AeS is exclusively confined to the order Stenoglossa (among marine invertebrates) are sufficiently interesting to make further investigation worthwhile. In addition, the discovery that *Nassarius* provides a rich source of sulphatase for use in steroid analysis warrants a more detailed investigation of the nature of the enzyme found in this animal. However, the specificity of the steroid sulphatase, present in the few available species that have been found to possess it, is such that the enzyme cannot be used to achieve complete hydrolysis of all the urinary steroid conjugates; the sulphates of $3\alpha{:}5\alpha$ steroids can still only be hydrolysed by chemical methods.

The writers are indebted to Mrs Ann Peace for valuable technical assistance; to the captains and crews of R.V.s 'Sula' and 'Sarsia' for collecting most of the test animals; to Mr N. A. Holme for many helpful discussions, and to Prof. A. Graham for his advice and interest.

SUMMARY

A study has been made of the distribution of β-glucuronidase, arylsulphatase and 'steroid sulphatase' in nine marine invertebrate phyla.

Species representative of all the phyla examined possess β-glucuronidase and arylsulphatase, but only certain gastropod molluscs, subclass Prosobranchia have a 'steroid sulphatase'. Two marine species, *Buccinum undatum* and *Nassarius reticulatus*, possess an enzyme of specificity similar to that of the sulphatase obtained from the land snail, *Helix pomatia*, in that it assists the hydrolysis of both aetiocholanolone and dehydro*epi*androsterone sulphates. However, the 'steroid sulphatase' prepared from three other marine species, *Patella vulgata*, *Patina pellucida* and *Littorina littorea*, has a higher specificity, assisting the hydrolysis of only the latter substrate. An enzyme that will effect the hydrolysis of androsterone sulphate has yet to be found.

Experiments with molluscs have shown that the β-glucuronidase and arylsulphatase activities of herbivorous species are, in general, greater than those of carnivores. Further experiments, using members of all the phyla examined, have shown that, compared with herbivorous and carnivorous species, animals

which feed on detritus are more often lacking in β-glucuronidase activity. However, this correlation between diets and enzymic activity is not found in experiments with 'steroid sulphatase' and there is evidence consistent with the view that this enzyme may not perform any physiological function related to the hydrolysis of steroid sulphates in the few species in which it has been found.

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A CHECK-LIST OF BRITISH MARINE HALACARIDAE (ACARI), WITH NOTES ON TWO SPECIES OF THE SUB-FAMILY RHOMBOGNATHINAE

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(Text-figs. 1–4)

Mites of the family Halacaridae are abundant on the sea shore, and in the sea down to considerable depths. Their identification is not an easy matter; there is no one account which can be used to identify all the British species, and the use of any one of the general accounts of European species, such as André (1946) or Viets (1936), by itself might easily lead to misidentification.

The purpose of the present list is to record the species which have so far been found around the British Isles, and to indicate sources of reliable descriptions of each species. A list of the British species of this family was given in a general list of British Acari by Turk (1953), and this has provided the starting point for the present list; no reference to occurrence in Britain before Turk's list is given, apart from one by Halbert (1920) which was left out by Turk. Twelve of the thirty-six species in the present list were not recorded by Turk. One species, *Halacarus zosterae* (Fab.), recorded by Turk has been omitted because the original description is quite inadequate to decide even which genus the creature should belong to. Eight species are known from British fresh water; these have not been included in the present list.

Only full species are given in this list, infra specific categories have been omitted. When the specific name is followed only by the author and date it indicates that the species was described from British material, and has not appeared in a general account of the group. The references in square brackets following the date indicate the source of a reliable description, while the succeeding references in rounded brackets give the authority for including the species as British.

The names in this list generally follow those given by Viets (1956) except that I have adopted Newell's (1947) classification of the Rhombognathinae, and the genus *Copidognathus* has not been divided into subgenera.

FAMILY HALACARIDAE Murray 1876

SUBFAMILY HALACARINAE Viets 1927

Gen. *Halacarus* Gosse, 1855

Subgen. *Halacarus* Gosse, 1855 s.str.
ctenopus Gosse, 1855 [Newell, 1947] (Turk, 1953)
actenos Trouessart, 1889 [Newell, 1947] (Turk, 1953)
bisulcus Viets, 1927 [Viets, 1936] (Spooner, 1959)

Subgen. *Thalassarachna* Packard, 1871 (= *Halacarellus* Viets, 1927)
basteri (Johnston, 1836) [Newell, 1947] (Turk, 1953)
southerni (Halbert, 1915)
areolatus (Halbert, 1915)
subterraneus (Schulz, 1933) [Newell, 1947][1]

Gen. *Copidognathus* Trouessart, 1888

granulatus (Hodge, 1863) [André, 1946, as *C. glyptoderma* Trs.] (Turk, 1953)
rhodostigma (Gosse, 1855) [André, 1946] (Turk, 1953)
loricifer André 1946 [André, 1946] (Turk, 1953)
fabricii (Lohmann, 1889) [André, 1946] (Turk, 1953)
tabellio (Trouessart, 1894) [André, 1946] (Turk, 1953)
lamellosus (Lohmann, 1893) [André, 1946] (Turk, 1953)
oculatus (Hodge, 1863) [André, 1946] (Turk, 1953)
gracilipes (Trouessart, 1889) [André, 1946] (Turk, 1953)
gibbus (Trouessart, 1889) [André, 1946] (Turk, 1953)

Gen. *Agauopsis* Viets, 1927

brevipalpus (Trouessart, 1889) [André, 1946] (Halbert, 1920)

SUBFAMILY POROHALACARINAE

Gen. *Caspihalacarus* Viets, 1928

hyrcanus Viets, 1928 [Viets, 1928*a*] (Green, 1956)

SUBFAMILY RHOMBOGNATHINAE

Gen. *Rhombognathus* Trouessart, 1888

notops (Gosse, 1855) [Newell, 1956] (Turk, 1953)
magnirostris Trouessart, 1889 [Newell & André, 1959][2]
lionyx Trouessart, 1900 [Newell & André, 1959][2]

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[1] This species has not previously been recorded from Britain. I have identified a single specimen from the Essex coast, near the mouth of the Thames.

[2] I have British specimens which agree with Newell and Andrés' recent redescription of these species.

Gen. *Isobactrus* Newell, 1947

setosus (Lohmann, 1889) [Newell, 1947] (Turk, 1953)
levis (Viets, 1927) [Newell, 1947] (Green, 1956*a*)
uniscutatus (Viets, 1939) [Viets, 1939] (Green, 1956*a*)

Gen. *Rhombognathides* Viets, 1927, emnd. Newell, 1947

pascens (Lohmann, 1889) [Newell, 1947] (Turk, 1953)
spinipes (Viets, 1933) [Willmann, 1952] (Green, 1956*a*)
seahami (Hodge, 1860) [Newell, 1947] (Turk, 1953)
trionyx (Trouessart, 1899) [André, 1946] (Turk, 1953)
merrimani Newell, 1947 [Newell, 1947] (Green, 1956*b*)
mucronatus (Viets, 1927) [Newell, 1947][1]

Gen. *Metarhombognathus* Newell, 1947

armatus (Lohmann, 1893) [Newell, 1947] (Green, 1956*b*)
nudus (Viets, 1928*b*) [Sokolov, 1952] (see below)

SUBFAMILY SIMOGNATHINAE

Gen. *Simognathus*

minutus (Hodge, 1863) [André, 1946 as *S. sculptus*] (Turk, 1953)

SUBFAMILY LOHMANELLINAE

Gen. *Lohmanella* Trouessart, 1901

falcata (Hodge, 1863) [André, 1946] (Turk, 1953)

Gen. *Scaptognathus* Trouessart, 1889

tridens Trouessart, 1889 [André, 1946] (Spooner, 1959)
trouessarti Halbert, 1915

Two of the mites recorded in the above list are of interest for two distinct reasons. Their occurrences in Britain represent considerable extensions of their known ranges, and their systematic status needs clarification, particularly in relation to the subdivision of the subfamily Rhombognathinae.

Metarhombognathus nudus (*Viets*)

In 1928*b* Viets described two species of the genus *Rhombognathus* from the Murmansk coast. Both species were found on the same alga, and one, *R. nudus*, was found only as the adult, while the other, *R. contectus*, was found

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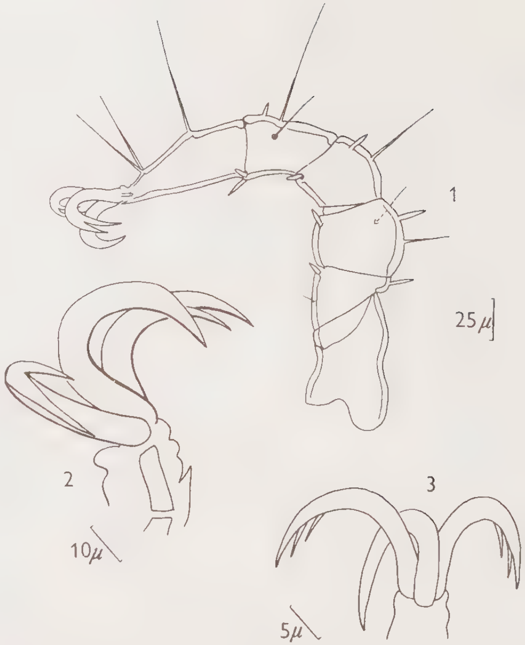
[1] Not previously recorded from Britain. I have a specimen from the Tees estuary, collected by Miss E. Clay.



Figs. 1–3. *Metarhombognathus nudus.* 1, Leg IV of adult. 2, terminal claws of leg I of adult. 3, terminal claws of leg I of larva.

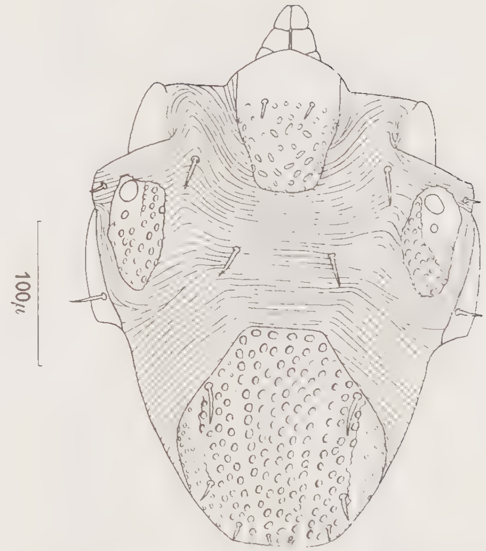


Fig. 4. Deutonymph of *Metarhombognathus nudus*, dorsal view of body. This specimen has a squarer posterior border to the anterior dorsal plate than most of the other specimens examined.

only as the deutonymph. Newell (1947), on the basis of his experience with a similar pair of forms, suggested that the two were in fact only one species. As Newell puts it 'It is highly improbable that two extremely closely allied forms (as shown by the unique structure of the lateral claws) could occupy the same habitat, both forms being numerous, and yet one be known only as the adult and the other only as the deutonymph'.

The two species have not apparently been recorded in the literature since the original descriptions and a repetition of these by Sokolov (1952), who still regards them as separate species. In Viet's (1956) register of the Halacaridae the two forms are maintained as separate species.

In March 1959 specimens agreeing with the description of *R. nudus* were found in small splash pools at the bottom of the cliffs at Cullercoats, Northumberland. The mites were very numerous in these pools, and all stages from larvae to adults were found.

The principal difference between *R. nudus* and *R. contectus* is that the dorsal plates of the former are small while those of the latter are large. When a random sample of twenty-five specimens from Cullercoats was examined in detail after clearing in lactic acid three specimens were found to be larvae. These had very small dorsal plates; the body length, from the front of the anterior dorsal plate to the posterior tip of the body, ranged from 216 to 223 μ. Five of the series were protonymphs, with small dorsal plates, and body lengths ranging from 223 to 295 μ. Seven deutonymphs, ranging in length from 350 to 380 μ, were found; these all had large dorsal plates and would be identifiable as *R. contectus*. Ten adults, with small dorsal plates, and having body lengths of 320–500 μ, completed the series.

This result of examining a random sample clearly indicates that *R. contectus* is the deutonymph of *R. nudus*. The latter name takes precedence owing to page priority. The finding that the protonymph has small dorsal plates like the adult is in agreement with Newell's description of the protonymph of *Metarhombognathus armatus* Lohmann, which has deutonymphs with large dorsal plates and adults with small dorsal plates. Newell has produced conclusive evidence that the deutonymphs of *M. armatus* with large dorsal plates are followed by adults with small dorsal plates by dissecting an adult from a quiescent deutonymph.

Further evidence that *R. contectus* is the deutonymph of *R. nudus* can be taken from the structure of the lateral claws. In the larvae, protonymphs and deutonymphs the lateral claws each carry two teeth on their inner borders (Fig. 3). This agrees with Viets figure of the claws of *contectus*. Nine of the adults had lateral claws with a single tooth on the inner border (Fig. 2), while one had two of its lateral claws with two teeth on their inner borders; it is noteworthy that this was the smallest of the adults. The loss of one of the teeth on the lateral claws appears to be normal when the adult stage is reached.

A further question is raised by the generic, or subgeneric, position of this species. The difficulty is that two different systems of classification have been proposed. Viets (1936, 1952, 1956) regards the subfamily Rhombognathinae as consisting of a single genus *Rhombognathus* Trouessart, which he subdivides into three subgenera. Newell (1947, 1953) regards the subfamily as comprising four genera. Using Viet's system the present species would be called *Rhombognathus* (*Rhombognathopsis*) *nudus*. I have, however, adopted Newell's system for reasons which will become apparent in the discussion of the next species.

Rhombognathides merrimani *Newell*

This species has been recorded in Britain from the following localities: Isle of Man (Green, 1956*a*); Skokholm Island, Pembrokeshire (Green, 1956*a*); Gwendraeth Estuary, Carmarthenshire, on *Cladophora*, and in the gut of *Gobius minutus* (Green, unpublished records). Previous to these records it was known only from North America.

Newell (1947) has given an admirably detailed description of this species, so that no further description is necessary here. The most important feature of this species, from a systematic point of view, is its occurrence in two varieties: *merrimani* having two claws on all its legs, and *needleri* having three claws on legs I and II, and two claws on legs III and IV. Apart from this difference in claw number the two varieties are identical. My British specimens include both varieties, and I am unable to find any other difference between them, so that I am convinced with Newell that they belong to the same species. Viets (1950, 1952, 1956) does not accept this; he regards the two forms as not only separate species, but belonging to different subgenera. This is necessary if Viet's classification of the Rhombognathinae is followed, since the subgenera are separated entirely on claw characters, as follows:

Leg	I	II	III	IV
Rhombognathus	2	2	2	2
Rhombognathides	3	3	2	2
Rhombognathopsis	3	3	3	3

If the two forms of *R. merrimanni* are conspecific, as Newell and I believe, then Viet's classification must fall, and a substitute be found. I have adopted Newell's system because it is based upon an analysis of a considerable number of characters and it groups together species which are obviously closely allied although they may differ in claw number. The alternative to Newell's system would be to keep the single genus *Rhombognathus* and not divide it further, this would be a negative attitude, resulting in a genus of some thirty species with no expression of affinities within the group.

The specimens of *Metarhombognathus nudus* were collected while running a marine biology course for students at the Dove Marine Laboratory, Cullercoats. It is a pleasure to thank Dr H. O. Bull and his staff for the facilities which they made available to us.

SUMMARY

A check list of British marine mites of the family Halacaridae is given.

Metarhombognathus nudus (Viets), hitherto known only from the Barents Sea, is recorded from Cullercoats, Northumberland. Evidence is presented which indicates that the form described as *Rhombognathus contectus* Viets is the deutonymph of *Metarhombognathus nudus.*

The known distribution of *Rhombognathides merrimani* Newell in Britain is summarized, and its systematic status in relation to the classification of the Rhombognathinae is discussed. It is recommended that Newell's classification of this subfamily be adopted.

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A NEW SPECIES AND GENUS OF BRACHIOPODA FROM THE WESTERN APPROACHES, AND THE GROWTH STAGES OF THE LOPHOPHORE

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From the Plymouth Laboratory

(Plate I and Text-figs. 1–14)

A new species and genus of brachiopod has been dredged by R.V. 'Sarsia' on three cruises to the Western Approaches of the English Channel and two to the La Chapelle Bank region. In general appearance it closely resembles *Dallina septigera* (Lovén) with which it appears to have been confused by Fischer & Oehlert (1891).

In 1956 it was obtained on 13 June at position 48° 33′ N., 10° 05′ W. at a depth of 570–770 fathoms, four specimens of shell length 17–25 mm were taken together with seven *D. septigera*.

On 3 May 1957 at position 48° 33′ N., 10° 01′ W., depth 580–680 fathoms, a specimen of shell length 22 mm and an entire shell, 19 mm long, were taken accompanied by one *D. septigera*. The bottom in both positions was complex, mostly stone, shell and coral gravel, with some mud and boulders. The brachiopods were attached to worn fragments of coral, shell or stone.

During a cruise in the winter of 1958 the new species and *D. septigera* were dredged in some numbers and on this occasion there was little mixing of the two species. On 28 November at position 48° 24′–26′ N., 10° 12′–08′ W., depth 540–650 fathoms, twelve specimens (shell length 3·6–24 mm) of the new species were taken: no *Dallina* occurred in this haul. On the 29 November at position 48° 32′–33′ N., 10° 10′–09′ W., depth 375–490 fathoms, amongst twenty-seven *D. septigera* was a single specimen (shell length 15 mm) of the new species and also six *Macandrevia cranium* (Müller). On 30 November at position 48° 38′ N., 9° 47′–48′ W., depth 510–550 fathoms, eighteen individuals (shell length 2.7–22 mm) of the new species were dredged together with a single *Dallina septigera*. On the same date in position 48° 39′–38′ N., 9° 45′–50′ W., 580–510 fathoms, one perfect specimen (shell length 19 mm), parts of a further three and one entire shell of the new species were obtained, together with one *D. septigera*, and the posterior ends of another two. On this 1958 cruise the new species was taken mainly attached to the dead region of growing coral, *Lophelia prolifera* (L.) Probably because the coral afforded shelter, a number of small specimens were found, the smallest being of shell length 2·7 mm and width 2·3 mm.

In the La Chapelle Bank region (47° 11′–14′ N., 6° 13′–11′ W., 625 fathoms) on 2 July 1959 one specimen (smashed) of shell length 7–8 mm was dredged, together with two *Dallina.*

From a second cruise in the La Chapelle Bank region (47° 37′ N., 7° 27′ W., 395 fathoms) on 11 July 1959, five of the new species (shell length 15–25 mm) were obtained in the same dredge haul as sixty-two *Dallina.* These brachiopods were from a chalky bottom and were attached to minute pieces of calcareous rock, and a few to living *Limopsis* (about 8 mm high) and *Limopsis* valves. In both species the pedicles were short. The specimens of the new species were of a broad and deep type; the four large ones had the following proportions: (1) 25 mm long, 24 mm wide, 19 mm deep (Pl. I, fig. 4); (2) and (3) 24 mm long, 22 mm wide, 17 mm deep; (4) 24 mm long, 22 mm wide, 16·5 mm deep. The new species is almost as variable in general shape as is *Dallina septigera.*

Altogether some forty-six specimens of the new species, shell length 2·7–25 mm, have been dredged.

All figures have been drawn with the aid of a camera lucida.

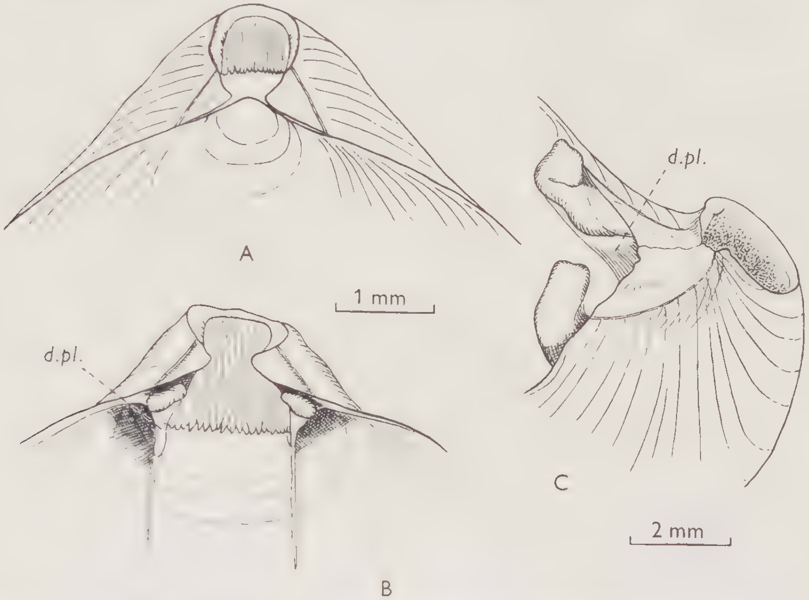
Fallax gen.nov.

Dallinid brachiopod with hinge teeth supported at all sizes by dental plates: deep, sessile pedicle collar. Loop passing through the growth stages characteristic of dallinids to reach the adult form, which is campagiform: ascending branches very broad, joined with the descending as far posterior as the junction with the septum, the two forming a gutter. Adult lophophore plectolophous. Spicules abundant, but not coarse, occurring in the lophophore, including the outer filaments, the body wall and over the mantle sinuses.

Fallax dalliniformis sp.nov.

The shell is variable in shape, elongate ovate to subpentagonal—rarely almost as wide as long—and broadest anteriorly (Pl. I). The two largest specimens were 25 mm long, 22·5 mm wide, 16·5 mm deep (Pl. I, fig. 5 and Text-fig. 5) and 25 mm long, 24 mm wide, 19 mm deep (Pl. I, fig. 4). The hinge line is curved; the shell is broadly sulcate to intraplicate; the test fairly thin and smooth; growth lines little marked; punctations somewhat finer and denser than in *Dallina septigera*; colour in the young creamy white, in adults fulvous or brownish owing to some deposit, possibly of manganese oxide. The beak is erect, the beak-ridges rounded. The deltidial plates are disjunct in the young (Text-fig. 1 A); fusion occurs at a shell length of some 10 mm and the pedicle opening is then entire; the line of fusion is generally apparent even in adults (Text-fig. 1 C). The otherwise circular foramen runs down in a small ‘v’ in front, the base of the ‘v’ being produced inwards as a small projection on each side (Text-fig. 1 C), into which runs a beak ridge; in individuals with short pedicles the projections are sometimes absent owing to abrasion. Dental plates support the strong hinge teeth at all sizes, vertical in the young (Text-fig. 1 B) they become curved in adults. (Dental plates are absent in *D. septigera* brought in by R.V. ‘Sarsia’, at least down to a shell length of 11·5 mm.) From the anterior corner of each dental plate a narrow ridge runs forward for a short distance. The deep sessile pedicle collar has a striated appearance owing to the longitudinal direction of the pits (Text-fig. 1B).

Cardinalia characterized by a platform which in adults tends to jut ledge-like over the rather thick septum (Text-fig. 2B, C). Even in the young the anterior edge of the platform is approximately at right angles to the septum, making a T-shape with it (Text-fig. 2A). (In *D. septigera* the cardinalia are less heavy, the hinge plates are generally markedly excavate, and in both young and adults the inner hinge plates curve gently to the thin-edged septum, giving a V-shaped outline.)



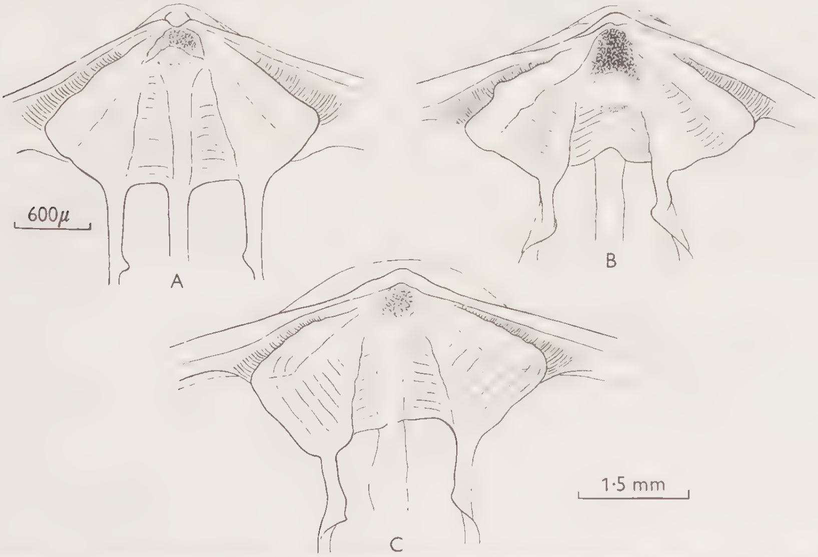
Text-fig. 1. *Fallax dalliniformis*. A, umbonal region of specimen of shell length 7·3 mm and width 6·8 mm. Deltidial plates are disjunct at this stage. B, beak of same specimen tilted somewhat on to its tip so as to reveal the dental plates, with ridges running forward from their anterior corners, and the sessile pedicle collar of striated appearance. C, beak of adult specimen of shell length 24 mm and width 20 mm. Oblique side view to show the shape of the unworn foramen and the conjunct deltidial plates. *d.pl.*, dental plate.

In young *Fallax dalliniformis* the crura arise from the inner socket ridges (Text-fig. 8): in adults their position shifts nearer the mid-line. No obvious crural bases, separating outer and inner hinge plates, as in *Dallina septigera*, can be distinguished, possibly because of the heavier cardinalia.

A cardinal process is absent; the diductor muscles are inserted on the floor of a small depression in front of the dorsal umbo (Text-fig. 2C), as in *Macandrevia cranium* (see Thomson, 1927, p. 240); in some individuals a small boss (Text-fig. 2B), in others a triangular elevation (Text-fig. 2A) is present in front of the depression.

In the brachial valve the median septum, rather broad posteriorly, extends forward for about three-quarters of its length.

The loop does not reach as far forward as the septum (Text-fig. 3). The crura are short (Text-fig. 2) and the crural processes small. The adult loop is campagiform, rather than terebrataliform, resembling that of *Campages furcifera* Hedley (Hedley, 1905). The descending branches are connected with the septum in all the large specimens obtained, and the very broad ascending branches are joined with the descending as far posteriorly as the junction with the septum, the two forming a gutter (Text-fig. 3). Some specimens, not always the largest, show a greater degree of resorption of the ascending branches than do others (Text-fig. 3 C, D), but even so, the ascending form a gutter with the descending as far backwards as the junction of the latter with the septum. The loop illustrated is very similar to that of a specimen of '*Dallina septigera*', 25 mm long figured by Fischer & Oehlert (1891, pl. v, fig. 9, *ac*). The transverse band is fairly wide from side to side, with a small bay in the posterior margin; it is wider than in *Campages furcifera*.



Text-fig. 2. *Fallax dalliniformis*. Cardinalia in specimens of different sizes: A, shell length 11·5 mm and width 11·0 mm; B, shell length 17 mm and width 14 mm; C, shell length 21 mm and width 17 mm.

The slender pedicle, very short in the young, reached a length of 11 mm in adults attached to large pieces of coral, but was short in those attached to rock and small objects.

The ventral pedicle muscle impressions are strongly marked and bounded laterally by ridges running from the anterior corners of the dental plates (Text-fig. 4A, B). A median elongated depression bounded laterally by raised ridges, marks the position of attachment of the diductor and adductor muscles; the impressions of the two are not clearly separated. The position of the ventral pedicle muscles relative to that of the adductor and diductor muscles changes with age, as does the relative size (Text-fig. 4A, B); at a shell length and width of 15 mm the surface of attachment of the ventral pedicle muscles is large (Text-fig. 4B). In the brachial valve the anterior and posterior adductor muscles are inserted separately on each side of the septum, the attachment of the two being almost in line with one another. The dorsal pedicle muscles are inserted on the hinge plate.

Two pairs of mantle sinuses are present in each valve.* In the brachial valve

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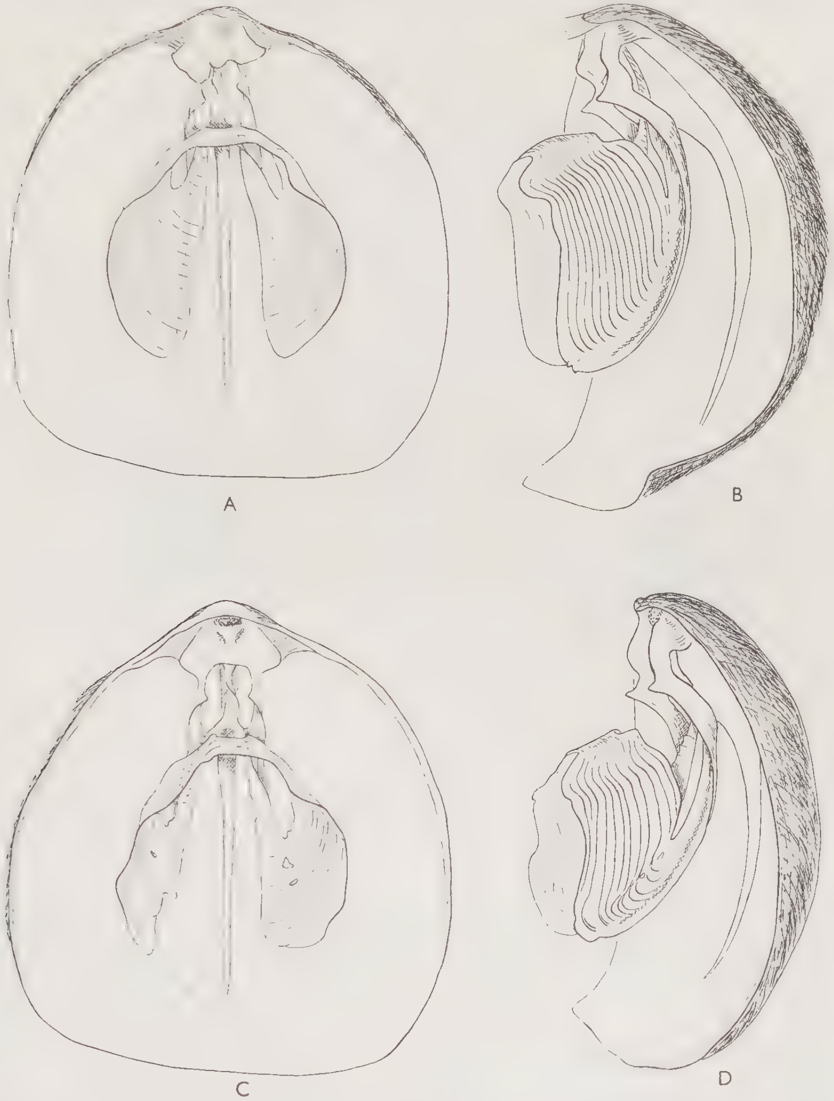
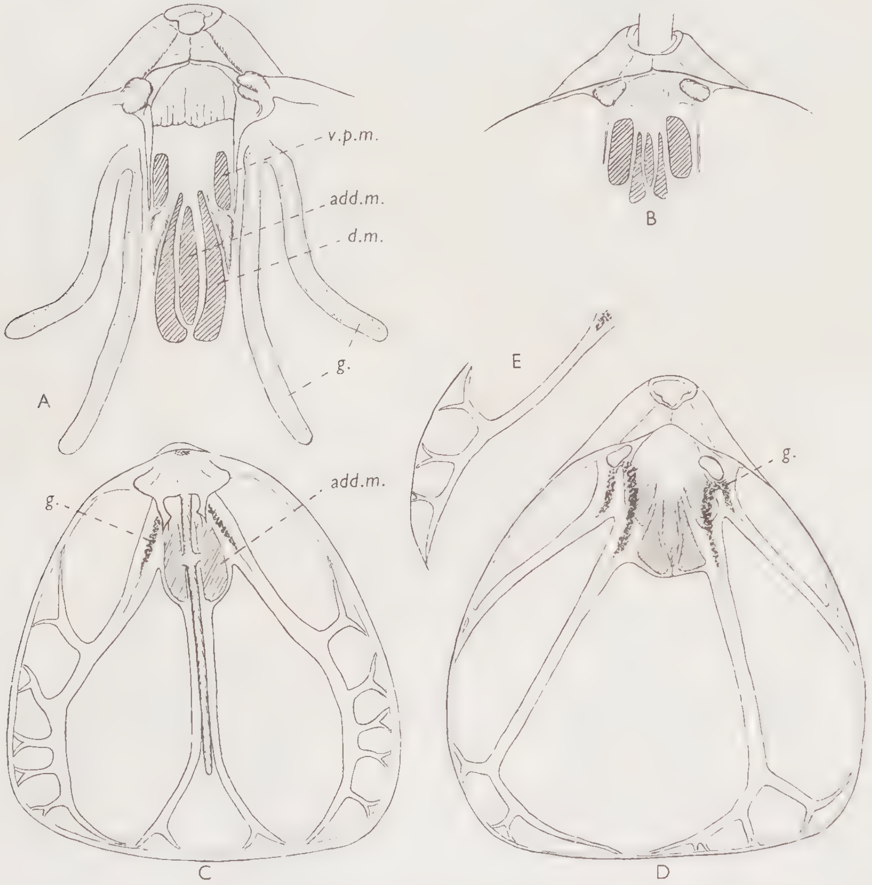
* The mantle sinuses were demonstrated by soaking the valves in an aqueous solution of Aniline blue for a few days.

(Text-fig. 4C) the inner pair run alongside the median septum to its anterior end and then diverge, each sinus branching near the mantle margin. The outer pair after their origin from the coelomic cavity run almost parallel with the valve edge giving off short exterior branches. This distribution is similar to that in *Dallina septigera* (see Fischer &



Text-fig. 3. *Fallax dalliniformis.* Interior of brachial valve of two specimens. A and B, of shell length 24 mm and width 20 mm; the left inner socket ridge is abnormally large. C and D, of shell length 21 mm and width 17 mm. The ascending branches show uneven development. The right descending branch had an abnormal growth anterior to the crural process, near an injury and mend to the valve: these abnormalities have been omitted.

Oehlert, 1891) except that the lateral sinuses appear to diverge more widely and in the only *Fallax* examined the first branch arose at some considerable distance from the coelomic cavity. In the pedicle valve (Text-fig. 4D, E) the inner pair diverge widely, and the inner branch of each is long, the two almost meeting on the mid-anterior margin. In *Dallina septigera* these sinuses are nearly parallel (Fischer & Oehlert, 1891,



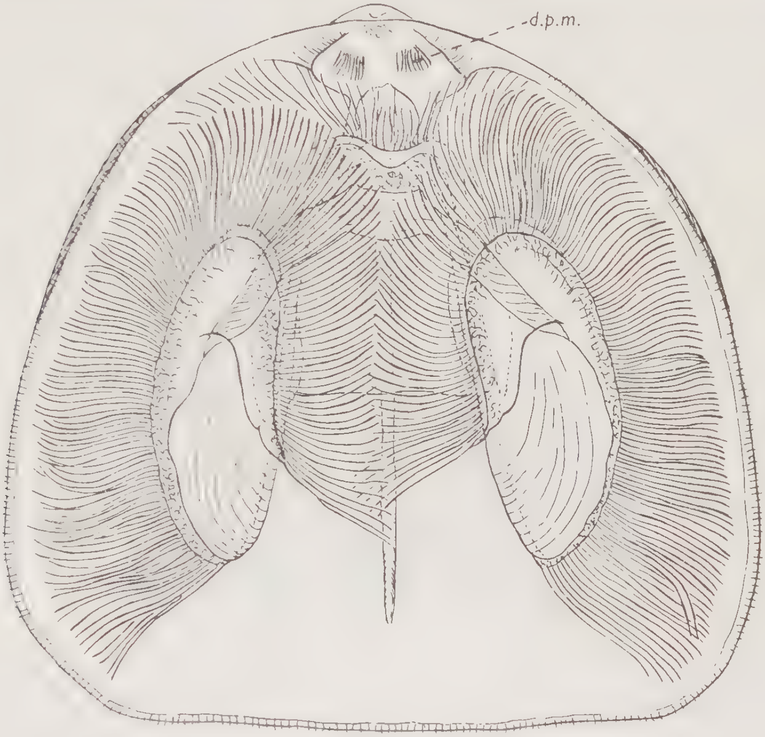
Text-fig. 4. *Fallax dalliniformis.* A and B, posterior region of pedicle valves showing muscle attachment: A, specimen 24 mm long; B, specimen of shell length and width 15 mm. Both tilted somewhat on to beak so as to show the dental plates. C–E. Distribution of mantle sinuses in a specimen 21 mm long. C, brachial and D, pedicle valves. E, an outer sinus of pedicle valve to show the end branches. *add.m.*, adductor muscles; *d.m.*, diductor muscle; *g.*, gonad; *v.p.m.*, ventral pedicle muscle.

and own work), as in *Macandrevia cranium* (see Hancock, 1858). Owing to the deep concavity of the ventral valve the outer branches of the lateral sinuses are not visible in ventral view, only when the valve is tilted on to its side (Text-fig. 4E).

The distribution of the gonad is as in *M. cranium* (see Hancock, 1858) and *Dallina septigera* (see Fischer & Oehlert, 1891). The sexes appear to be separate, but sectioning has not been carried out, and it is possible that alternation in the production of sex cells may occur.

The mantle setae are short and closely set in the adult.

The adult lophophore is plectolophous, with an alternating series of inner and outer filaments, except behind the mouth where some thirty-six are in single series. Spicules are present in the lophophore, including the outer, grooved filaments to about half of their length, in the body wall and over the mantle sinuses (Text-figs. 6, 7), in this differing strikingly from *D. septigera*. The spicules are fairly fine, of irregular spidery branching, especially those in the body wall and over the mantle sinuses (Text-fig. 7). The deep band of mucous cells at the base of the filaments when full of spherules hides the spicules in that position (see Text-fig. 14).

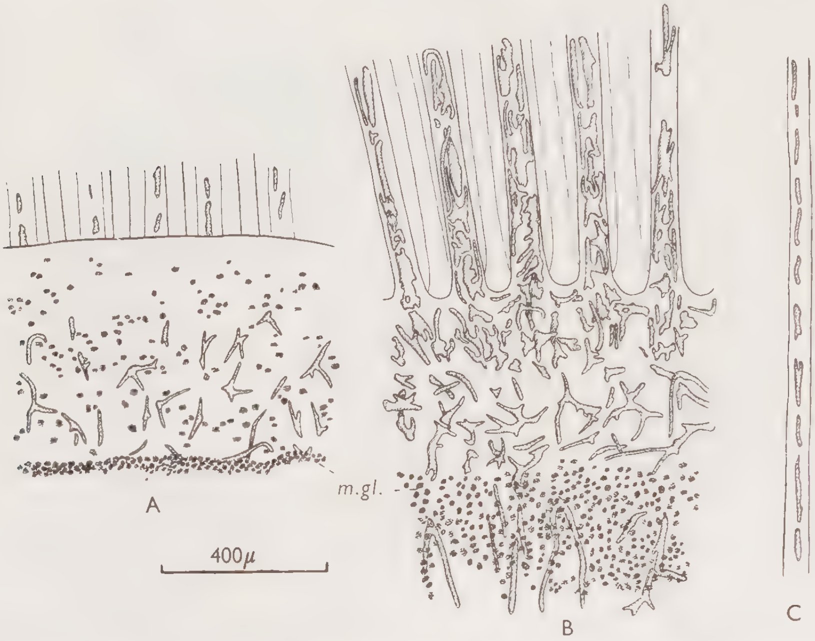


Text-fig. 5. *Fallax dalliniformis* of shell length 25 mm and width 22·5 mm. Brachial valve with plectolophe drawn living: alimentary canal omitted. Loop added after clearing in cedar wood oil. *d.p.m.*, dorsal pedicle muscle.

Fallax dalliniformis lacks the two carmine pigment spots found in connexion with the preoesophageal ganglion in certain brachiopods, as does also *Dallina septigera* and *Macandrevia cranium*.

The ciliary feeding mechanism is as described for *M. cranium* by Atkins, (1956). In large living specimens the valves may gape anteriorly as much as 6 mm.

With practice *Fallax dalliniformis* can be distinguished externally from *Dallina septigera* by the difference in the shape of the pedicle opening. The presence of abundant spiculation is the character by which living *Fallax dalliniformis* is most quickly distinguished from *Dallina septigera*, but in specimens long preserved in alcohol or in formalin, unless neutralized, these tend to disappear and then the presence of dental plates, deep sessile pedicle collar and the differences in cardinalia and loop clearly separate the new species from *D. septigera*. Although *D. septigera* can be described as lacking spicules, in one individual a few minute, widely scattered spicules were found in the lophophore after a careful search. Dall (1871, p. 16) has recorded the presence of a very few exceedingly delicate spicules in the floor of the greater mantle sinuses in *D. floridana*.



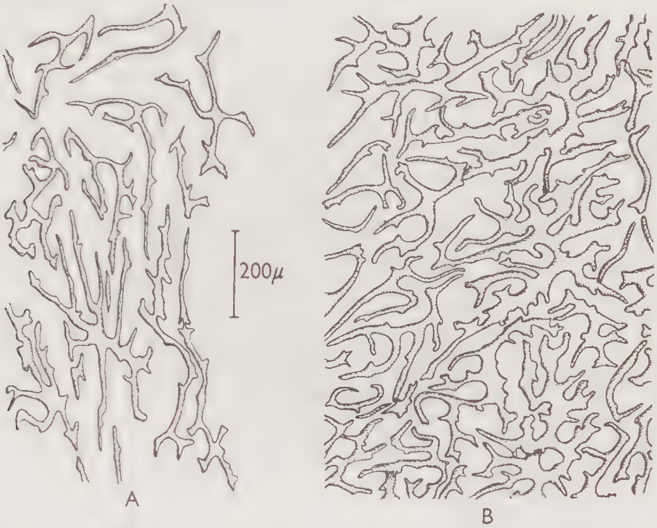
Text-fig. 6. *Fallax dalliniformis.* Spiculation of the lophophore of a specimen 25 mm long and 22·5 mm wide (same specimen as shown in Text-fig. 5). A, lip of food groove; B, spicules in outer grooved filaments and between their bases and the loop, seen from the abfrontal surface, C, outer grooved filament at extreme distal region of spiculation. *m.gl.*, mucous gland cells.

Type locality

Western Approaches to the English Channel in an area 48° 24′–39′ N., 9° 45′–10° 12′ W., at a depth of 375–770 fathoms.

Type specimens

As the first specimens obtained in 1956 have been damaged in the post, the single *Fallax dalliniformis* of 3 May 1957, 48° 33′ N., 10° 01′ W., 580–680 fathoms has been chosen as the holotype (Pl. I, fig. 1). Two specimens of 28 November 1958, 48° 24′–26′ N., 10° 12′–08′ W., 540–650 fathoms (Pl. I, figs. 2, 3) and one of 11 July 1959, 47° 37′ N., 7° 27′ W., 395 fathoms (Pl. I, fig. 4) have been chosen as paratypes. These specimens will be deposited in the British Museum (Natural History) when they can be conveyed there safely.



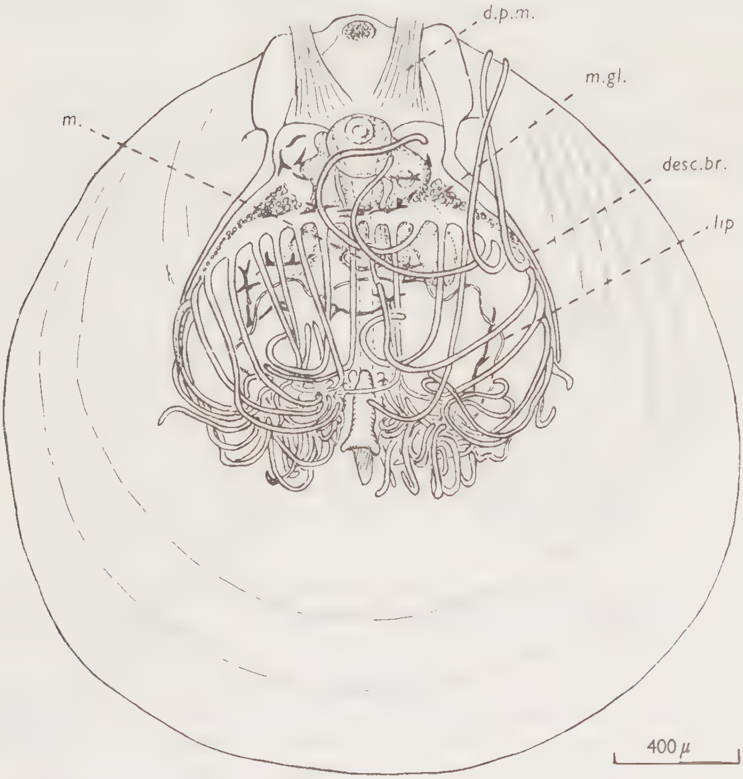
Text-fig.7. *Fallaxdalliniformis.* Spiculation of (A) body wall of individual 22 mm long and 16 mm wide; of (B) mantle over the male gonad of specimen 21 mm long and 15·5 mm wide.

Breeding

The breeding season is not known; it may possibly be in the winter months. In June 1956, of the four specimens obtained, the sex of the smallest, of shell length 17 mm, could not be determined. Two of shell length 24 and 25 mm were males with tailed sperm in the gonad, and the fourth, of shell length 21 mm, was a female. In both sexes the gonad was small. In November 1958 seven males (shell length 16–24 mm) had tailed sperm in their gonads. Two specimens (shell length 19 and 24 mm) had gonads of fair size; in the other five they were small. In five females of shell length 18–22 mm although the ova were large and round, the gonads were mostly small. In six of shell length 9–20 mm no gonad was discernible, and in a further two of shell length 20 and 22 mm sex could not be determined without sectioning. The four large *F. dalliniformis* of July 1959 had the gonads visible through the shells which were not opened.

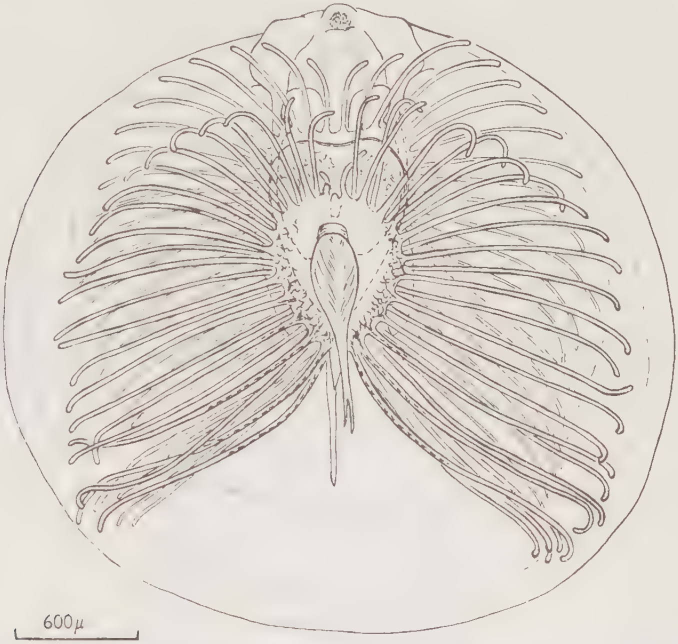
GROWTH STAGES OF THE LOPHOPHORE AND LOOP

Some few immature individuals have been found allowing of certain of the growth stages to be described. The smallest, of shell length 2·7 mm and width 2·3 mm already showed spicules at the bases of the filaments, on the brachial membrane of the schizolophous lophophore and in the body wall. In this individual it appeared as though the widely curved descending branches were continued by long spicules; it was, however, impossible to be certain that these were not fractured ends of the branches. If they were, then the descending branches extended about half way around the lophophore. (It is not intended to imply that the loop is formed by fusion of spicules, but possibly they support the lophophore until the descending branches are fully formed.) The septum posteriorly bore a small hood of somewhat irregular shape.



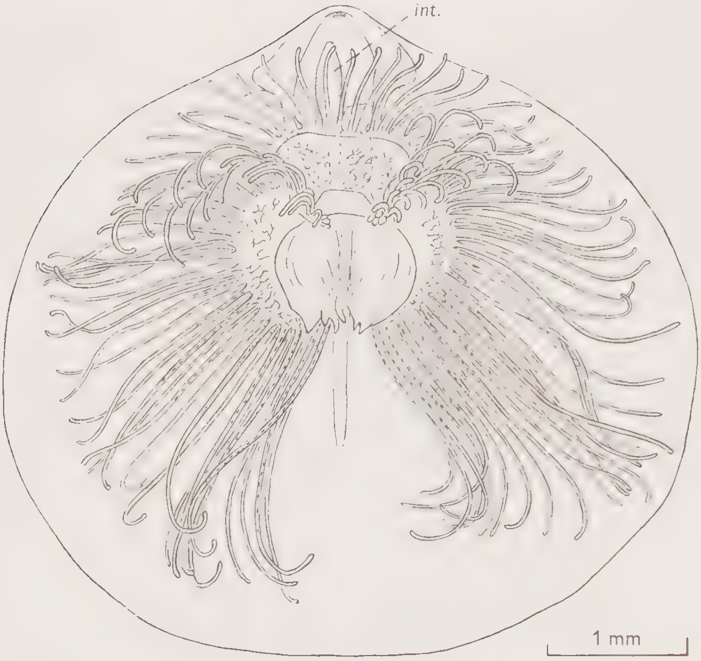
Text-fig. 8. *Fallax dalliniformis* of shell length 2·9 mm and width 2·4 mm. Brachial valve with schizolophe; the descending branches (*desc.br.*) are incomplete. Preserved specimen. *d.p.m.*, dorsal pedicle muscle; *lip*, edge of lip of food groove; *m.*, mouth; *m.gl.*, mucous gland cells. Spicules are indicated.

In a slightly larger specimen of shell length 2·9 mm and width 2·4 mm the descending branches were easier to distinguish and extended rather more than half way around the lophophore, which was of the broad-based terebratellacean type, set low on the dorsal mantle (Text-fig. 8). When complete, the descending branches of the loop, following the outline of the lophophore, would be almost circular, as in *Macandrevia cranium* (Atkins, 1959*b*); it is only in later stages that they make an acute angle with the septum. Unlike the smaller specimen, the median septum had as yet no recognizable hood; anteriorly it bore two short blunt projections. In both these small individuals the septum was connected with the cardinalia by a low ridge.

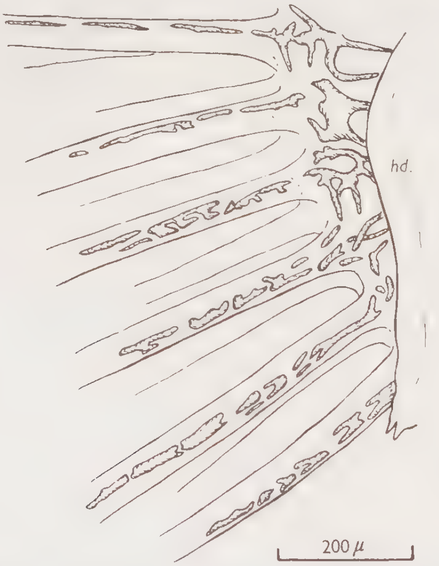


Text-fig. 9. *Fallax dalliniformis* of shell length 3·6 mm and width 3·3 mm. Brachial valve with late schizolophe, drawn living, with the loop added after clearing in cedar wood oil. The descending branches are complete: the hood is open posteriorly. The gut is omitted.

From these two specimens it is evident that the descending branches arise early in development, although not as early as in *M. cranium*, and that the septum is more forward in development than in the latter species, in which a hood does not appear until after the completion of the descending branches (Atkins, 1959*b*). That the descending branches grow from the crura only can unfortunately not be proved, as the necessary stage is wanting. It is, however, probable, for although the descending branches were long, no lateral projections were present on the septum.



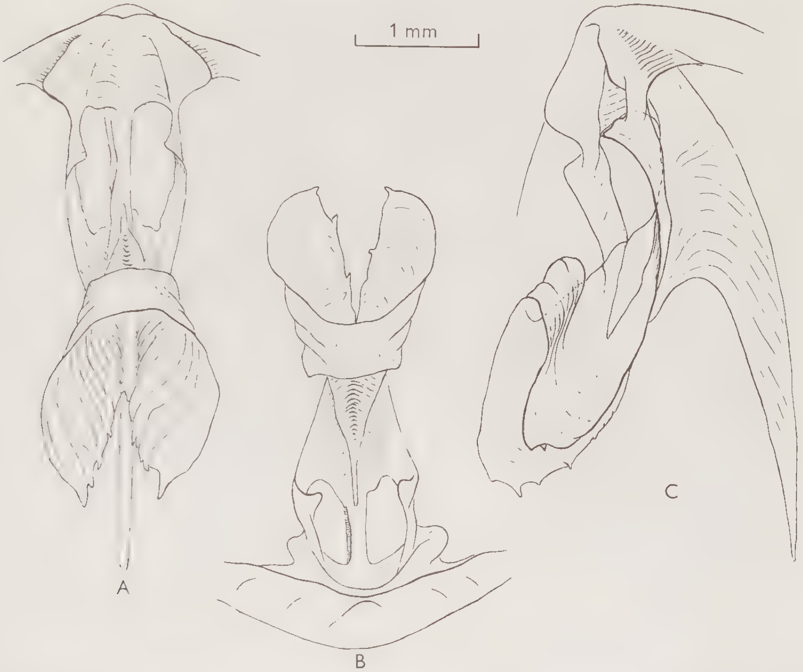
Text-fig. 10. *Fallax dalliniformis* of shell length 5·4 mm and width 5·1 mm. Brachial valve with zygolophe, drawn living, with the loop added after clearing in cedar wood oil. *int.*, intestine.



Text-fig. 11. *Fallax dalliniformis*. Part of the lophophore shown in Text-fig. 10, enlarged to show the spicules. *hd.*, hood.

At a shell length of 3·0 mm and width of 2·7 mm the lophophore was late schizolophous and the lateral arms were already deflected. The descending branches joined the septum at an acute angle: the hood was long, narrow and entire; the septum was produced into a long spine anteriorly. Spicules were now present in a few of the outer filaments situated at the anterior ends of the lateral arms.

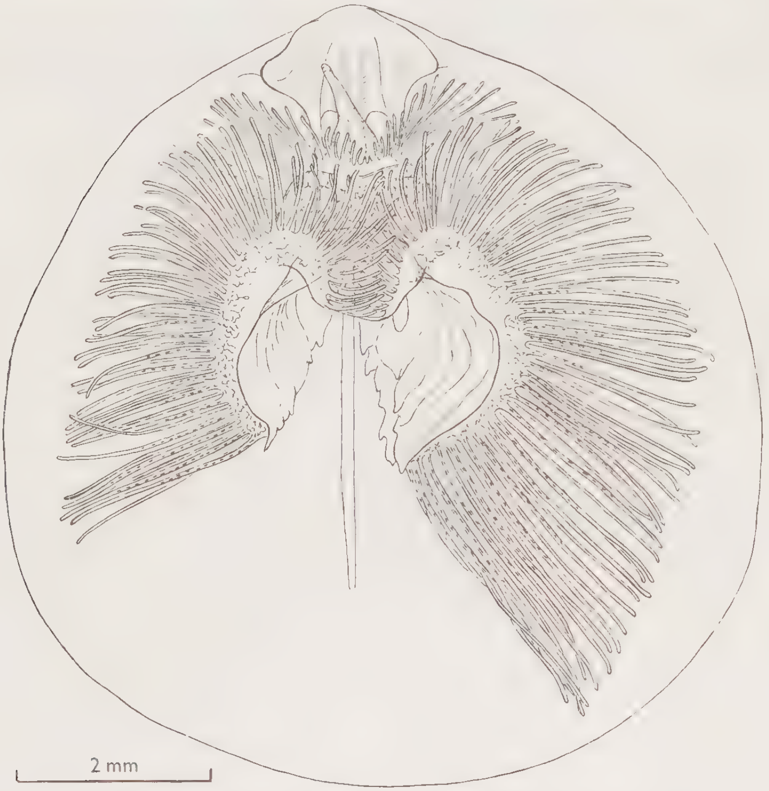
Three specimens of nearly the same size and of about the same stage of development of the lophophore—late schizolophous to very early zygolophous—were obtained. In one of shell length 3·6 mm and width 3·2 mm, the angular hood was the least developed of the three, the posterior end being entire. Anteriorly the septum had spinous projections. The hood of a slightly smaller individual of shell length 3·6 mm and width 2·7 mm, was fairly broad and somewhat asymmetrical; the posterior end had undergone resorption. Anterior spinous projections were short and from their appearance it is possible that the hood had been damaged in life. The hood of the third individual of shell length 3·6 mm and width 3·3 mm was long, fairly narrow with high sides and was open posteriorly (Text-fig. 9). Anteriorly the septum was produced into long spines. It is evidently at about the size of these three



Text-fig. 12. *Fallax dalliniformis.* Loop of specimen 7·3 mm long and 6·8 mm wide. A, ventral view; B, as seen when the valve is standing on its anterior edge; C, side view.

specimens, when the lophophore is late schizolophous, that resorption of the posterior end of the hood occurs.

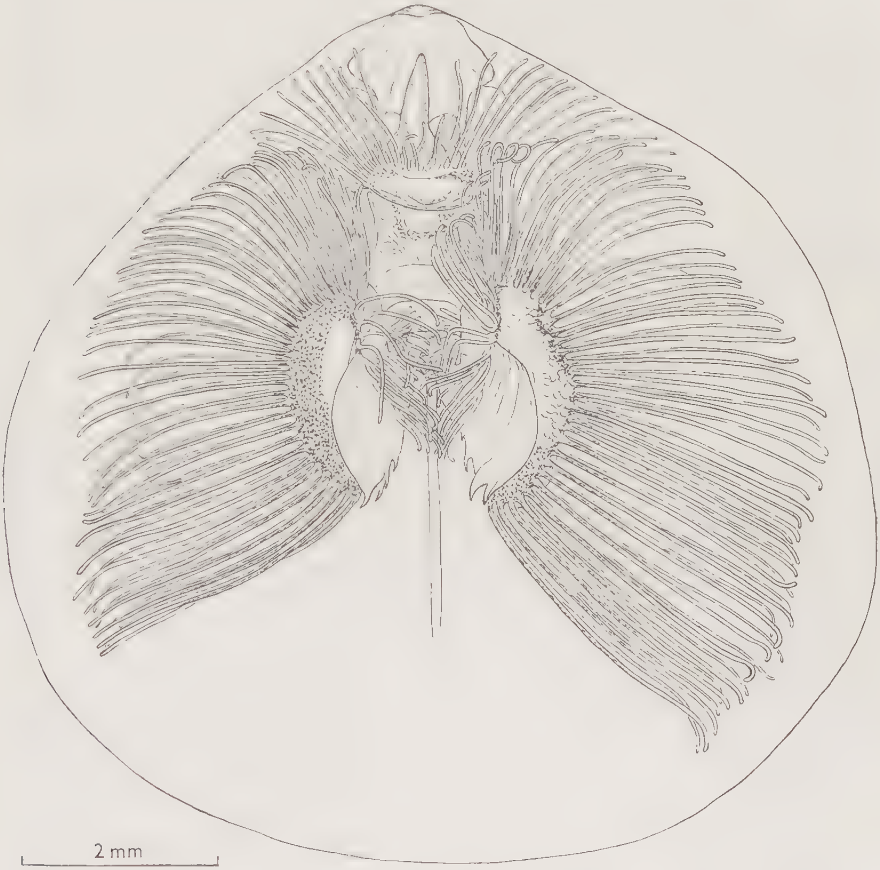
At a shell length of 4·8 mm and width of 4·4 mm the lophophore was early zygolophous; the hood, somewhat asymmetrical in shape, had widened; the transverse band was distinct. Long anterior spines still remained.



Text-fig. 13. *Fallax dalliniformis* of shell length 8·7 mm and width 7·8 mm. Brachial valve with early plectolophe; the lateral arms most unevenly developed. Spicules are indicated.

The lophophore was zygolophous at a shell length of 5·4 mm and width of 5·1 mm. The hood, or ascending branches of the loop, had widened greatly: slight anterior bifurcation was evident with short spines bordering it (Text-fig. 10). Spicules in part of the lophophore are shown enlarged in Text-figure 11. The loop extended to the middle of the valve.

A specimen of shell length 7·3 mm and width 6·8 mm was without flesh, so that three aspects of the loop could be drawn (Text-fig. 12). The hood was deeply divided anteriorly, the sides of the bifurcation being spinous. The sides of the hood, or broad ascending branches, were attached to the ventral surface of the septum as far backward as the posterior attachment of the descending branches, the two sides forming a ventrally facing gutter, extending beyond the transverse band of the loop. This is a slightly younger stage than that shown by Friele (1877, pl. iv, fig. 13) of *Dallina septigera* at a shell length of about 6·0 mm and is very similar.



Text-fig. 14. *Fallax dalliniformis* of shell length 9·2 mm and width 8·9 mm. Brachial valve with early, almost symmetrical, plectolophe. The position of the mucous cells on the lophophore is indicated where these are full of spherules, as on the left lateral arm and certain regions of the right arm. Spicules are only visible where the mucous cells have shed their contents.

At a shell length of 8·7 mm and width of 7·8 mm the lophophore was early plectolophous, with some three-quarters turn to the spiral arm (Text-fig. 13). In this specimen the lateral arms were most unequally developed. Spines were present along the inner, dorsal edges of the ascending branches. Resorption had begun posteriorly in the larger, right ascending branch. Spicules were present over the oesophagus, contrary to the condition in *Platidia* (Atkins, 1959*a*).

In an individual of shell length 9·2 mm and width 8·9 mm with lateral arms almost symmetrically developed (Text-fig. 14), the early plectolophe had rather more than a complete turn to the median arm. The anterior region of the loop retained its spinous character. Mucous cells were present in a deep band at the bases of the filaments; those on the right arm had largely shed their contents: when full of spherules they hide the spicules.

The loop in the adult extends to the extremities of the lateral arms: the spinous projections are lost (Text-fig. 5, p. 77).

DISCUSSION AND AFFINITIES

It seems almost certain that Fischer & Oehlert (1891) had *Fallax dalliniformis* but failed to separate it from *Dallina septigera*. The individual of their fig. 9 *r–u*, pl. iv, is possibly *Fallax*. According to them the teeth of *D. septigera*: 'sont supportées, chez les jeunes, par des cloisons rostrales, qui s'atténuent avec l'âge et disparaissent complètement chez l'adulte, il n'exist ni doublure sous-apicale, ni septum médian'. The smallest *D. septigera* examined, 11·5 mm long, for the present work had the teeth unsupported by dental plates, although in adults they had somewhat swollen bases. It is perhaps possible that Fischer & Oehlert having *D. septigera* and *Fallax dalliniformis* mingled, made their statement to explain the presence of dental plates in some of their specimens and absence in others. It is most unfortunate that a *Dallina septigera* of shell length 5·0 mm was lost before being examined for dental plates, for it would have settled the question of their presence in the young.

Referring to previous descriptions of the growth stages of the loop of *D. septigera*, Fischer & Oehlert (1891, p. 71) said 'nous représentons seulement le stade dit *térébratelliforme* (pl. iv, fig. 9 *aa*, *ab*) qui est le plus persistant et le plus instructif au point de vue du groupe. Chez les spécimens ayant de 10 à 20 millimètres de long, l'appareil descendant, au-dessous des pointes crurales, s'élargit rapidement et se soude bientôt au septum médian; à partir de ce point les branches descendantes sont constituées par une lamelle étroitement repliée sur elle-même en forme de gouttière et dont la partie externe persiste seule dans les appareils arrivés à leur complet état de développement.' Thus according to them the gutter is formed entirely by the descending branch. It has been shown (p. 73–4) that this 'térébratelliforme' stage of Fischer & Oehlert's '*D. septigera*' is the adult loop of *Fallax dalliniformis*—indeed their fig. 9*aa* and *ab*, pl. iv represent a somewhat idealized loop of *F. dalliniformis* with the cardinalia of that species—and the gutter is formed not by the descending branch alone, but by the fused descending and ascending branches, as in *Campages furcifera* Hedley. Thomson (1927, fig. 74*f*) reproduced their figure as a terebrataliform stage. In *Dallina septigera* dredged by R.V. 'Sarsia' the loop is entirely free from the septum from a shell length of about 13 mm., and the ascending and descending branches are fused for a variable, but generally short, distance anteriorly (Atkins, 1960).

Fallax dalliniformis obtained in November 1958 from coral exhibited abnormalities of shell and internal structure, including asymmetry of shell valves (Pl. I, fig. 2), loop (see Text-fig. 13) and cardinalia (Text-fig. 3A). Asymmetry of the shell resulting from injury was probably caused by the crowded branches and polyps of the coral; that of the loop and cardinalia may follow, or possibly be caused by predatory animals. As mentioned previously these *Fallax* from coral tended to have pedicles of up to 11 mm long.

It is impossible to place this new species in *Dallina* because of the presence at all sizes of dental plates, deep sessile pedicle collar, the difference in cardinalia and the presence of abundant spiculation; the presence of dental plates precludes it being placed in *Japanithyris*, a genus of which little is known; a new genus, *Fallax*, has therefore been created.

Fallax dalliniformis no doubt should be placed in the Dallinidae and most probably in the Dallininae, as now constituted because of its loop form, presence of dental plates, early development of the descending branches of the loop, probably growing from the crura only, and anterior bifurcation of the septum in the early stages, with spines on the loop. But while it is said (Thomson, 1927, p. 231) of the Dallininae that spicules are occasionally present, but never abundant, they are abundant, although not coarse, in *F. dalliniformis*, which in this differs from any genus of Dallininae so far described. It is possible that spiculation is present in other genera of the subfamily and has escaped notice, as apparently by Fischer & Oehlert (1891) in certain of their specimens of '*Dallina septigera*'. Mr G. F. Elliott tells me that among specimens labelled *D. septigera* in the British Museum (Natural History) one dried specimen with T-shaped cardinalia shows glistening membranes suggesting strong spiculation.

In the presence of spicules *Fallax dalliniformis* approaches *Laqueus*, but the adult loops are entirely different, as is the folding. In addition to spicules it agrees with *Laqueus* in the presence of dental plates, sessile pedicle collar and absence of cardinal process, all characters in which it also agrees with certain of the Dallininae. Thomson (1927, p. 259) records of *Laqueus* 'small spicules present over the pallial sinuses, but not extending to the body-wall or lophophore'. In the few *L. californianus* (Küster) from Puget Sound, North America, that I examined, long delicate spidery spicules were present not only over the pallial sinuses, but also in the body wall, at the bases of the filaments behind the mouth, and between the two carmine pigment spots and the transverse band; I was unable to find them in the filaments or between their bases and the loop. Incidentally this species of *Laqueus* possesses two carmine pigment spots near the preoesophageal ganglion.

Although the adult loop of *Fallax dalliniformis* resembles that of *Campages*, and especially that of *C. furcifera* Hedley, *Fallax* differs from *Campages* in possessing dental plates at all ages, lacking a cardinal process and possessing abundant spiculation.

My thanks are due to the Captain and crew of R.V. 'Sarsia' who dredged the brachiopods, and especially to Dr A. J. Southward and Mr G. R. Foster who were in charge of the scientific work, and who took great care of these delicate brachiopods during the journeys back to the laboratory. Those from the second cruise to the La Chapelle Bank region were very kindly picked out and cared for by Mr H. Gill (Cambridge University). I am indebted to Mr A. C. G. Best for the photographs in the plate: faults in blacking out the background are my responsibility. Mr G. F. Elliott most kindly read the manuscript. The work was done while occupying a London University table.

SUMMARY

A new species and genus, *Fallax dalliniformis*, of dallinid brachiopod is described from the Western Approaches to the English Channel, in the area 48° 24′–39′ N., 9° 45′–10° 12′ W., depth 375–770 fathoms, and from the La Chapelle Bank region 47° 11′–37′ N., 6° 11′–7° 27′ W., 395–625 fathoms. It is homoeomorphic with *Dallina septigera* (Lovén), with which it occurred in some dredge hauls. It is characterized by the possession of dental plates to the hinge teeth, deep sessile pedicle collar, a campagiform loop in the adult, spiculation in the lophophore, the body wall and over the mantle sinuses: in all these characters and in the cardinalia it differs from *D. septigera*. Shell length 25 mm.

Growth stages of the lophophore from schizolophous to plectolophous are described. The loop passes through the growth stages characteristic of dallinids as far as the campagiform stage, which in this species is the adult loop.

EXPLANATION OF PLATE I

Fallax dalliniformis sp. et gen.nov.

Fig. 1 A–D. Dorsal, ventral, lateral and frontal views of the holotype, 22 mm long, 19 mm wide and 15·5 mm deep. May 1957, 48° 33′ N., 10° 01′ W.; 580–680 fathoms.

Figs. 2–4. Paratypes to show variation in shape.

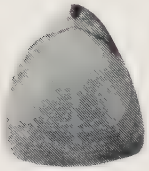
Fig. 2 A–D. Specimen 21 mm long, 15·5 mm wide and 15 mm deep. November 1958, 48° 24′–26′ N., 10° 12′–08′ W.; 540–650 fathoms, on coral. Foraminifera attached to pedicle.

Fig. 3 A–D. Specimen 24 mm long, 20 mm wide and 17 mm deep. Obtained on same date and from same position as previous specimen.

Fig. 4 A–D. Specimen 25 mm long, 24 mm wide and 19 mm deep. July 1959, from chalk bottom, 47° 37′ N., 7° 27′ W.; 395 fathoms.

Fig. 5 A, B. Ventral and frontal views of specimen 25 mm long, 22·5 mm wide and 16·5 mm deep. (The same specimen of which the brachial valve with plectolophe is shown in Text-fig. 5; the loop is now smashed.) June 1956, 48° 33′ N., 10° 05′ W.; 570–770 fathoms.

(All photographed while in water. Approximately natural size.)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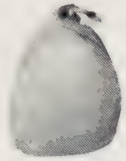
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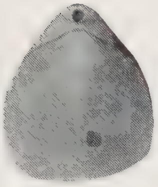
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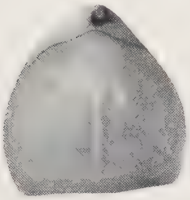
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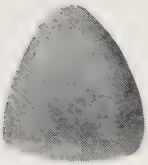
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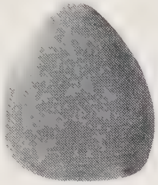
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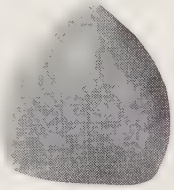
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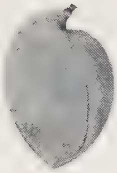
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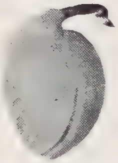
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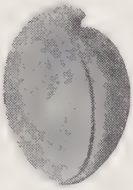
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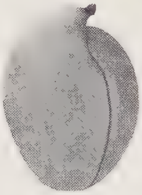
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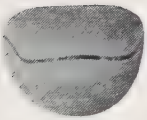
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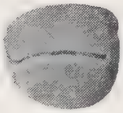
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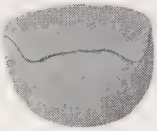
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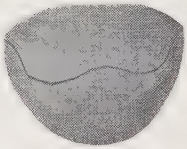
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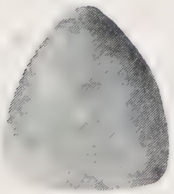
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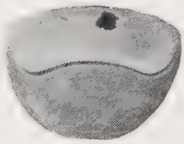
5 B

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A NOTE ON *DALLINA SEPTIGERA* (LOVÉN), (BRACHIOPODA, DALLINIDAE)

By D. Atkins, D.Sc.
From the Plymouth Laboratory

(Plate I and Text-figs. 1–5)

The discovery of a homoeomorph, *Fallax dalliniformis*, of *Dallina septigera* (Lovén) dredged with that species (Atkins, 1960) and, it is believed, sometimes confused with it, certainly by Fischer & Oehlert (1891), has made a brief redescription desirable. During the present work more than a hundred *D. septigera* of shell length 5–31 mm have been obtained, and most of them examined internally.

The original description in Latin—without figures—of *Dallina septigera* (= *Terebratula septigera*) was by Lovén in 1846 (p. 183). Unfortunately his description does not now clearly separate his species from *Fallax dalliniformis*, except perhaps his failure to mention the presence of dental plates, pedicle collar and spiculation. It is doubtful how much weight can be attached to this, for on the same page he failed to mention the presence of dental plates in *Macandrevia cranium*. He gave the length as 28 mm, width as 21·5 mm and depth as 17 mm.

The Stockholm Natural History Museum, the most likely Museum to possess Lovén's type specimen, unfortunately does not have it, and it is probable that he did not designate one. The Museum, however, does possess old collections of dried shells of this species from Norway and the North Sea, which Lovén probably studied. Through the kindness of Dr H. Mutvei a large specimen from these was loaned to me: he stated that it is not known with certainty whether it was collected before or after 1846—the date of publication of Lovén's paper. This specimen (Pl. I, fig. 2A–D), of length 29 mm, width 22 mm and depth 18 mm, has no dental plates; the pedicle collar is a narrow rim, slightly more marked than in some of the *Dallina septigera* dredged by R.V. 'Sarsia'. The loop is attached to the crura only and is somewhat stouter than in my specimens of about the same size. The ascending branches are wide, narrowing abruptly to the transverse band, which is deeply embayed anteriorly, and less so posteriorly. The band is narrower (antero-posteriorly) than in the majority of 'Sarsia' specimens, in which it generally resembles that figured by Sars (1878, Tab. 1, fig. 2*g*): the depth of the band, however, is variable. The inner hinge plates form a V with the septum. Dr Mutvei mentioned that the shells comprising these old collections have similar external shape.

Gray (1853, p. 59) was the next to describe *D. septigera* under the name *Waldheimia septata*. He seems to have given an abstract of Lovén's description with the same shell measurements: he also failed to provide figures.

In 1855 (p. 441) Davidson described *D. septigera* from a single specimen originally in the possession of S. Hanley, and gave figures of the dorsal, lateral and frontal views of the entire shell. These figures show the typical shape of the beak and pedicle opening of the species, and his failure to mention dental plates makes it almost certain that he had it. His statements that the deltidium was in two pieces and the beak ridges well defined would seem to be errors.

Dall in 1871 was apparently the first to give a figure of the loop, and from this it is obvious that he was dealing with *D. septigera*. His figure clearly shows that in the adult the loop was attached to the crura only, it also shows the V-shaped junction of the inner hinge plates with the septum. He stated: 'hinge plate longer than wide, anterior point passing forward between the crura'. He gave the length as 1·20 in., width as 1·10 in. and depth as 0·80 in., and mentioned that this large specimen originated from Jeffreys. Although he does not refer to the absence of dental plates in *D. septigera* he (1921, p. 359) remarked of *D. floridana* 'there are no props to the dental plates', apparently meaning no props to the teeth.

Friele (1877) described certain of the growth stages of the loop of *D. septigera*. That he had this species appears certain, for he figured the inner hinge plates running in a V to the septum and showed a young stage (size not given) in which the branches of the loop were free from the septum, thus distinguishing it from *Fallax dalliniformis*. The crura in his specimens—drawn with camera lucida—have the appearance of being somewhat shorter than in the 'Sarsia' *Dallina septigera*.

Jeffreys (1878, pp. 407–9) described *D. septigera* under the name *Terebratula septata* Philippi. He noted that in the full grown state the loop is attached only to the hinge plate: from this it is clear that he had *D. septigera*. His specimens, the largest of which was an inch and three-tenths long, were obtained by the 'Porcupine' expeditions. The dredgings in the Western Approaches to the English Channel from which Jeffreys obtained some of his specimens were near the positions where R.V. 'Sarsia' dredged, it therefore seems possible that he may have obtained *Fallax dalliniformis* as well as *Dallina septigera*.

Sars (1878, p. 11 and pl. I, fig. 2), under the name *Waldheimia septata*, gave good figures of the entire shell in dorsal, lateral and frontal view and also the brachial valve in ventral and side view. From the two latter views in particular it is evident that Sars was dealing with *Dallina septigera*: the hinge plates run in a V to the septum and the loop is attached to the crura only, while the descending and ascending branches are joined for but a short distance anteriorly. The crural processes end in characteristic slender curved points.

He gave the length as 36 mm: the adult he figured was somewhat longer than broad.

Davidson in his Linnean Society Monograph (1886) again described *D. septigera* (= *Waldheimia septigera*). He repeated that the deltidium was in two pieces, but omitted his earlier statement concerning well-defined beak ridges. He reproduced some of Sars's figures, but gave a new one of the ventral view of the adult loop (pl. 11, fig. 4) and added an anterior view (pl. 11, fig. 6). The figures show that the adult loop is attached to the crura only and is therefore not that of *Fallax dalliniformis*. Moreover, he stated (p. 57): 'the connection between the process of the lamellae and the septum is severed in a specimen 6 lines in length, and in a specimen 8 lines in length the lamellae are separated and the character of the loop is that of adult *Waldheimia*'. He gave the length as 1 in. 8 lines, that is approximately 42 mm.

Davidson (1886), in discussing Jeffreys' mistaken naming of *Dallina septigera* as *Terebratula septata* Philippi, mentioned that Seguenza had examined the perfect loop in several adult examples of Philippi's *T. septata* from the Pliocene and found it to be three times attached. Thomson (1927, p. 251) placed *septata* in his new genus *Japanithyris*.

Mr G. F. Elliott most kindly examined all the specimens of '*Dallina septigera*' in the British Museum (Natural History) and from his description there is evidently a mixture of *D. septigera* and *Fallax dalliniformis*, but the specimens of the latter may have been added since Davidson's time.

As already mentioned (Atkins, 1960) it seems clear that Fischer & Oehlert (1891) had both *Dallina septigera* (called by them *Magellania septigera*) and its accompanying homoeomorph, and that their description is compounded of characters of the two. Of their figures on pl. iv, fig. 9*aa*, *ab* of the brachial valve of a specimen of shell length 14 mm is almost certainly *Fallax dalliniformis*, and it is possible that fig. 9*r*–*u*, exterior views of a shell, is also. Fig. 9*x*–*z* is the loop of *Dallina septigera*, but although it would seem by the dotted line connecting fig. 9*x* and 9*y* that *y* is the loop of *x* enlarged, yet although 9*x* shows the V-shaped meeting of hinge plates with septum, fig. 9*y* shows the meeting T-shaped; this is perhaps the artist's error; in this figure there is also some appearance of transverse connecting bands between the descending branches and the septum, almost obliterated, whether intentionally or not, by shading. On pl. v, fig. 9*ac* of the loop of a specimen 25 mm long is almost certainly of *Fallax dalliniformis*.

Certain of the statements of Fischer & Oehlert apply to *Dallina septigera* only, namely: (1) 'il n'existe ni doublure sous-apicale...' in the ventral valve; (2) 'plateau cardinal...acuminé en avant'; (3) 'mince septum médian'; and (4) loop connected to crura only as in their pl. iv, fig. 9*x* and *z*.

Their statement that the 'dents sont supportées, chez les jeunes, par des cloisons rostrales, qui s'atténuent avec l'âge et disparaissent complètement chez l'adulte' needs confirmation. In *D. septigera* dredged by R.V. 'Sarsia' dental plates are absent from a shell length of at least 11·5 mm, whereas in *Fallax dalliniformis* they are present at all the sizes obtained.

Fischer & Oehlert (1891, p. 69) mentioned that they had several times found the 'terebratelliforme' stage in individuals of large size appearing fully adult. These were almost certainly *F. dalliniformis* Atkins, 1960.

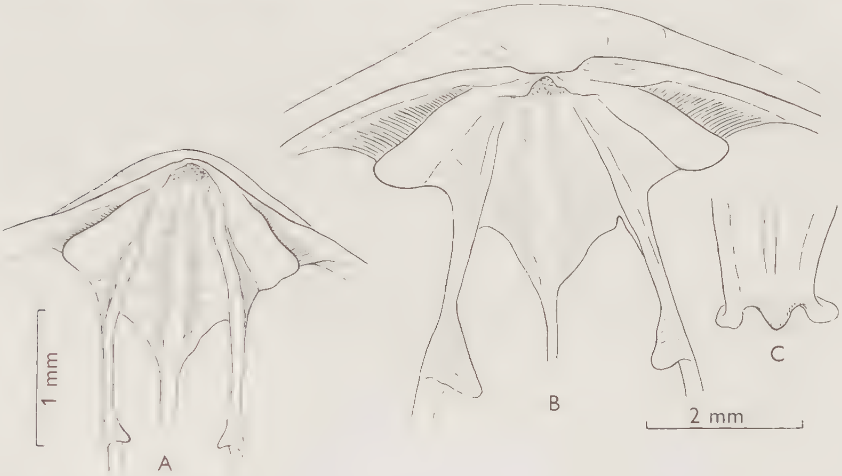
Thomson (1927, pp. 252–3) evidently based his description of *Dallina septigera* at least partly on that of Fischer & Oehlert (1891, pp. 64–71) and therefore mentioned certain characters absent in *D. septigera* but present in its homoeomorph *Fallax dalliniformis*. The description of *Dallina septigera* given here is based on Thomson, omitting those characters which belong to *Fallax dalliniformis* and emphasizing those which distinguish it from the latter species.

The presence of dental plates is said to be characteristic of the Dallininae, but as Thomson (1927, p. 178) remarked in a footnote *Dallina* itself is an apparent exception, although—evidently following Fischer & Oehlert (1891)—he stated that they were present in the young stages of *D. septigera*, but absent in adolescence (p. 238). Hatai (1940, pp. 316–18, 319, 320–21, 322) noted the absence of dental plates in *D. raphaelis* (Dall), *D. raphaelis albida* (Dall), *D. obessa* Yabe and Hatai and *D. elongata* Hatai. He (p. 320) omitted to mention their absence in *D. triangularis* Yabe and Hatai, but inferred it by saying 'interior features as in *D. raphaelis*'. Dall (1921, p. 359) had previously remarked of *D. floridana* 'there are no props to the dental plates nor septum in the pedicle valve'. This is difficult to follow unless he intended to write there are no props to the teeth. Hatai (1940) in his description of Japanese species of *Dallina* noted the large complete circular foramen, although in *D. raphaelis albidus* it was said to be somewhat transverse. In *D. raphaelis*, *D. raphaelis albidus* and *D. elongata* he described a short sessile striate pedicle collar, but omitted mention of this in *D. obessa* and *D. triangularis*, although it is implied in the latter. All the Japanese species have a symphytium with or without a raised median ridge.

All figures have been drawn with the aid of a camera lucida.

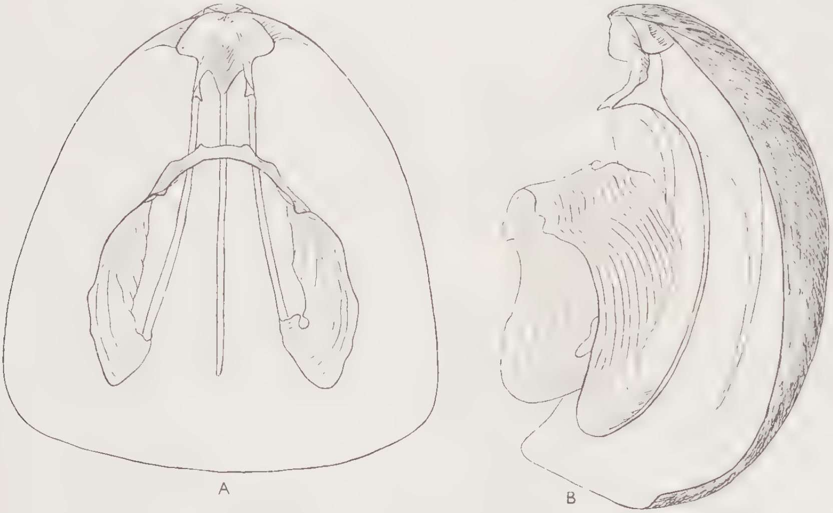
Dallina septigera (Lovén)

Shell large, very variable in shape, generally subpentagonal, broadest anteriorly (Pl. 1, fig. 2A–D), but varying from elongate triangular (Pl. 1, fig. 1A–D) to equilateral triangular, in which the width may slightly exceed the length (Pl. 1, fig. 3A–D). Hinge-line curved, shell broadly sulcate to intraplicate, test thin, smooth. Beak prominent, erect, without beak ridges, foramen large, *circular*, complete, ? mesothyrid, attrite. Symphytium with raised median ridge: it is complete at a shell length of 11·5 mm and possibly earlier. *Hinge teeth unsupported by dental plates*, at least from a shell length of 11·5 mm, the smallest examined, that of 5 mm shell length having been lost; in adults the bases of the teeth somewhat swollen. *Pedicle collar represented merely* *by a narrow inner rim* about 1 mm deep. Cardinalia characterized by excavate hinge-plates supported by the median septum, and separable into inner and outer hinge plates by the crural bases, which are not united laterally with the socket ridges (Text-fig. 1 A, B and Thomson, 1927, fig. 26). In a large specimen of shell length 27 mm, width 28 mm and depth 20 mm (Text-fig. 3) the hinge-plates were only slightly excavate. *The anterior edges of the inner hinge-plates form a long* V *with the septum.* Cardinal process absent in the young, tendons of diductor muscles attached in a rounded depression (Text-fig. 1 A): in adults the area of attachment consists of a median depression with on each side a small elevation (Text-fig. 1 B), the end of the tendon being tripartite (Text-fig. 1 C). Median septum thin, fairly high posteriorly, gradually lessening in height anteriorly, and extending forward to three-quarters the length of the valve. *Adult loop dalliniform*, attached to the crura only, extending beyond the septum (Text-fig. 2). (Elliott's (1953, p. 269) statement that 'in *Dallina* itself the early adult loop is quite often still terebrataliform, the dalliniform pattern being achieved later' was evidently based on Fischer & Oehlert's (1891) description combining characters of both *D. septigera* and *Fallax dalliniformis*.) The crura are long in the young (Text-fig. 1 A); they appear less so in the adult (Text-fig. 1 B) possibly because of the increase in size of the crural processes; these are large and produced into long slender curved points (Text-fig. 2 B), well shown by Sars (1878, pl. 1, fig. 2*g*, refigured by Davidson, 1886, pl. 11, fig. 5) and Fischer & Oehlert (1891, pl. IV, fig. 9*z*). In the adult the ascending branches of the loop are wide, but free from the slender descending branches except for a variable but generally short distance anteriorly: their inner, dorsal, margins are slightly irregular where resorption has occurred. The transverse band of the loop is variable in depth antero-posteriorly, but is generally deep, with a slight posterior bay (Text-fig. 2) and occasionally a pronounced anterior one.

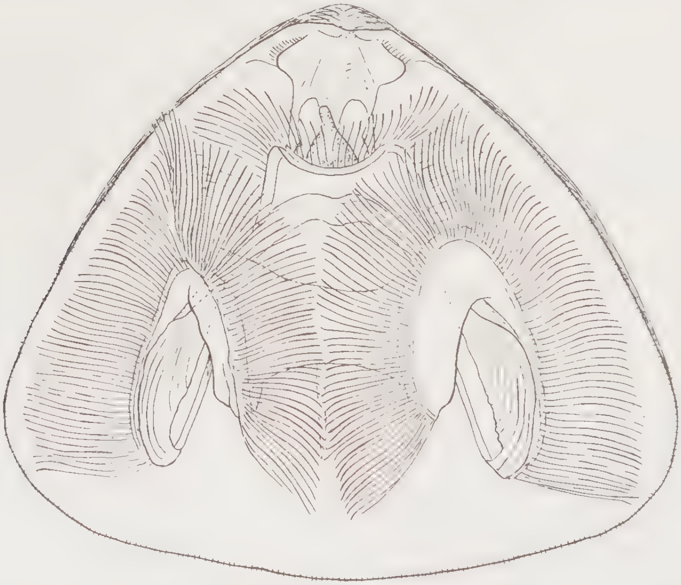


Text-fig. 1. *Dallina septigera*. Cardinalia of two specimens: A, of shell length 11·5 mm, width 10 mm; B, of shell length 24 mm, width 21·5 mm; C, dorsal end of tendons of diductor muscles removed from specimen shown in B.

Muscular impressions not strongly marked. Four pallial sinuses present in each valve. Adult lophophore plectolophous (Text-fig. 3), with nineteen to twenty-four filaments in single series behind the mouth. The specimen figured is one of two in which the width slightly exceeded the length. Spicules mostly absent, when present are minute and widely scattered (Atkins, 1960).



Text-fig. 2. *Dallina septigera*. Interior of brachial valve of specimen of shell length 29 mm, width 25 mm and depth 20 mm. A, ventral and B, side views.

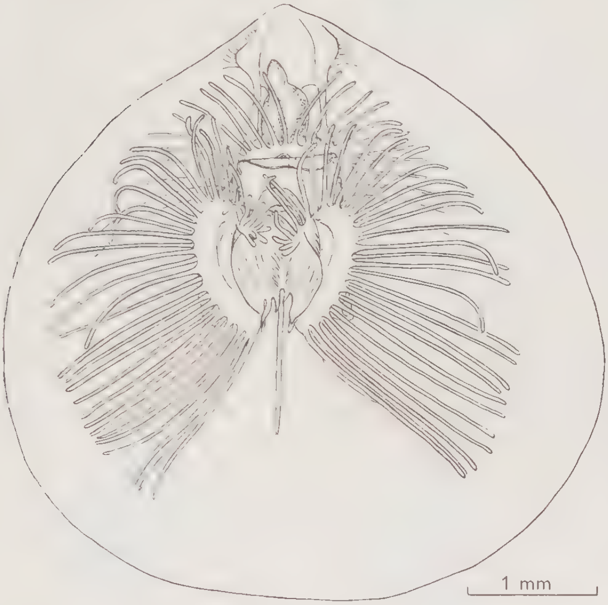


Text-fig. 3. *Dallina septigera*. Brachial valve with plectolophous lophophore of male individual of shell length 27 mm, width 28 mm and depth 20 mm: one of two specimens obtained in which the width exceeded the length.

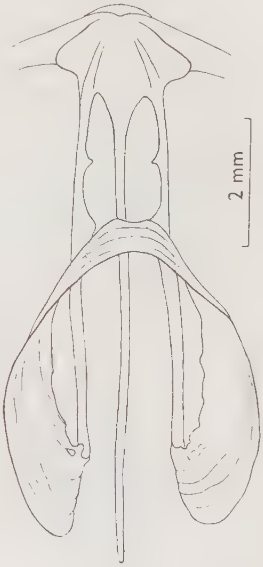
Dallina septigera agrees with *Macandrevia cranium* (Müller) and *Fallax dalliniformis* in lacking the two carmine pigment spots found in certain other brachiopods in connexion with the preoesophageal ganglion.

The ciliary feeding mechanism is as described for *Macandrevia cranium* by Atkins (1956).

The largest specimen obtained was 31 mm long, 25 mm wide and 20 mm deep: it came from position 47° 37′ N., 7° 27′ W. at a depth of 395 fathoms.



Text-fig. 4



Text-fig. 5

Text-fig. 4. *Dallina septigera*. Brachial valve with zygolophous lophophore of specimen of shell length 5 mm (brachial valve 4·5 mm long). The lip is turned forwards exposing the mouth.

Text-fig. 5. *Dallina septigera*. Ventral view of loop of specimen of shell length 13 mm and width 11·5 mm.

Two specimens in which the width slightly exceeded the length had the following dimensions: (1) 27 mm long, 28 mm wide, 20 mm deep (Pl. 1, fig. 3); (2) 23 mm long, 24 mm wide, 15 mm deep.

Breeding. In the seven *Dallina septigera* (shell length 12·5–26 mm) obtained in June 1956 and the single specimen of May 1957 (shell length 24 mm) the gonads were too immature for the sex to be determined without sectioning. Of those obtained in November 1958, twenty-four were examined for sex: ten (shell length 18–27 mm) were males, tailed sperm being present in all; three (shell length, 23, 24, 25 mm) had the gonad well developed. Four (shell length 16–24 mm) were females; two of these (shell length 16 and

24 mm) had large rounded eggs. In ten individuals (length 11·5–22 mm) no gonad could be discerned. Most of the *D. septigera* of July 1959 had the gonad visible through the shell, but in those examined sex products were immature.

GROWTH STAGES OF THE LOPHOPHORE

A number of growth stages of the loop were figured by Friele (1877), the smallest with brachial valve 4·5 mm long. The youngest *D. septigera* obtained during the present work had a shell length of 5·0 mm, with the brachial valve 4·5 mm long. It was thus of about the same size and its loop (Text-fig. 4) at about the same stage of development as Friele's fig. 12, pl. iv; its lophophore was zygolophous. In Friele's figure it is to be noted that the crura are considerably shorter than in the specimen dredged by R.V. 'Sarsia'. No *D. septigera* were obtained between a shell length of 5·0 and 11·5 mm. At the latter size, and also at a shell length of 12·5 mm, a slight connexion was present between each descending branch of the loop and the septum, the brachial support being as in Friele's fig. 16. The lophophore was early plectolophous. From a shell length of 13–17 mm a small triangular projection on each descending branch marked its former connexion with the septum (Text-fig. 5). As mentioned on p. 93 Davidson (1886) found that the connexion between the descending branch and the septum was severed in a specimen six lines in length, that is 12·7 mm.

Acknowledgements are due to the persons mentioned in Atkins (1960), and to London University for the use of a Table.

SUMMARY

Following the discovery of a homoeomorph, *Fallax dalliniformis* Atkins 1960, of *Dallina septigera* (Lovén) occurring with that species and confused with it by Fischer & Oehlert, *D. septigera* has been redescribed.

EXPLANATION OF PLATE I

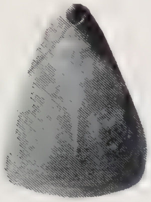
Dallina septigera (Lovén), to show variation in shape.

Fig. 1, A–D. Dorsal, ventral, lateral and frontal views of specimen 26 mm long, 18 mm wide and 17 mm deep, from position 48° 39′–38′ N., 9° 45′–50′ W.; depth 580–510 fathoms. The light circular area on the pedicle valve marks the former position of a *Verruca*.

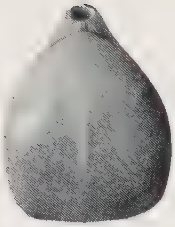
Fig. 2, A–D. Dorsal, ventral, lateral and frontal views of a specimen 29 mm long, 22 mm wide and 18 mm deep from the Stockholm Natural History Museum. Locality Norway and North Sea. The symphytium had evidently been injured and later repaired by the animal.

Fig. 3, A–D. Dorsal, ventral, lateral and frontal views of specimen 27 mm long, 28 mm wide and 20 mm deep, from position 48° 32′–33′ N., 10° 10′–09′ W.; depth 375–490 fathoms.

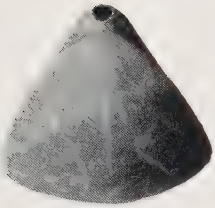
Figs. 1 and 3 photographed while in water; Fig. 2 photographed dry. Approximately natural size.



1 A

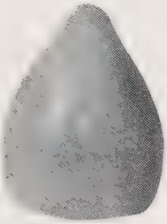


2 A



3 A

1 B



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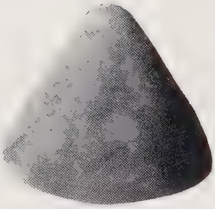

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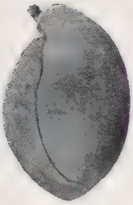

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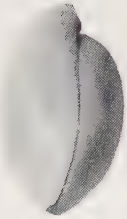

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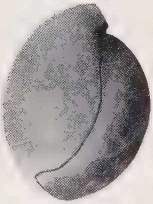

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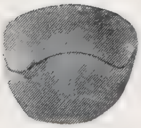

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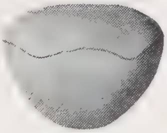

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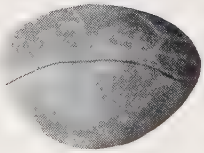

3 D

(*Facing p.* 98)

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ENTIONELLA MONENSIS SP.NOV., AN ENTONISCID PARASITE OF THE SPIDER CRAB *EURYNOME ASPERA* (PENNANT)

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Marine Biological Station, Port Erin, Isle of Man

(Text-figs. 1–8)

The family Entoniscidae (Isopoda-Epicaridea) is included in the superfamily Bopyrina, which comprises the families Bopyridae, Dajidae and Entoniscidae. The Bopyridae are parasitic in the branchial cavity or on the abdomen of decapods, mainly Macrura and Anomura. The Dajidae occur in the incubatory chamber or on the dorsal surface of mysids and euphausiids, and rarely on Brachyura. The Entoniscidae are found in the visceral cavity of Anomura and Brachyura (an exception is *Synalpheion*, in a macruran, Coutière 1908), surrounded by a membrane of host origin, and communicating with the branchial cavity of the host by a pore. Together with this internal habitat the family has extreme morphological specialization. Females of the Bopyridae have distinct thoracic segmentation and well-developed peraeopods; in the Dajidae the peraeopods are distinct, but segmentation is less evident; in adult females of the Entoniscidae, however, the peraeopods consist of only the enlarged oostegites, with rudimentary endopodites in some species, and the thorax has only traces of segmentation.

Giard & Bonnier (1887) considered that entoniscids were morphologically and physiologically external parasites, that the sheath was formed by invagination of the body wall of the host, and that the external medium circulated within it. However, Miyashita (1941) considers that there is little, if any, circulation, and shows that in *Entionella fluviatilis* Miyashita the fluid within the sheath is indistinguishable from the haemolymph of the host. Veillet (1945) has shown that in *Portunion maenadis* (Giard) the younger stages are totally internal; the host secretes a sheath, which only later develops an opening to the exterior. The family may therefore be considered truly endoparasitic.

The Entoniscidae have been studied in only a few areas, and it is probable that only a small proportion of the total species have been recorded. The most recent survey of the family is by Shiino (1942). There are thirty-one known species, which are distributed as follows.

Europe, 12 spp.; South America—Atlantic coast, 5 spp.; North America—Atlantic coast, 3 spp.; North America—Pacific coast, 1 sp.; Japan, 10 spp.

Two species have been recorded previously from British waters, *Pinnotherion vermiforme* from *Pinnotheres pisum* and *Portunion maenadis* from *Carcinus maenas* (Marine Biological Association, 1957, pp. 206–7).

Material examined

102 specimens of *Eurynome aspera* were collected offshore around the south of the Isle of Man, and two were infected by the entoniscid described below. A male crab, carapace length 17·5 mm, dredged on 7 November 1958 in 40 m approximately 6 km west of Fleshwick contained two ripening female parasites. A second male, carapace length 16·5 mm, dredged on 24 February 1959 in 65 m approximately 9 km west of Calf Sound contained an ovigerous female and a male.

Genus **Entionella** Miyashita 1941

Female. First oostegite with well-developed ascendant, lateral and recurrent lobes. Thorax without ovarian processes. Heart on third abdominal segment. Convoluted pleural lamellae on first and second abdominal segments only.

Male. Peraeopods jointed. Thoracic terga expanded laterally as flat plates. Abdominal segments 1–4 with hyposphenians ('crochets ventraux médians', Giard & Bonnier, 1887).

Entionella monensis sp.nov.

Description

Female. The following description is of the ovigerous specimen (Fig. 2). The cephalogaster is bilobed and swollen; ventrally it bears the first and second antennae, which are rounded lobes flanking the mouth (Fig. 3, *an* 1, 2). Posterior to these are the maxillipedes (Fig. 3, *mxp*), each having a bilobed prominence, which bears a free flattened third lobe dorsally. The respiratory folds (*rf*) or 'corps spongieux' of Giard & Bonnier (1887) are small and simple, and ventral to the maxillipedes.

The thorax is dull orange in colour, of even width and without ovarian processes. The peraeopods are represented only by five pairs of oostegites which arise dorsally, the reduced dorsal surface of the thorax lying between their bases (Fig. 4, *dst*). Oostegites 2–5 form the brood chamber, but this is open and eggs lie between the oostegites and the host membrane. Oostegite 1 is large and has three lobes; the ascendant and lateral lobes are both folded and hood-like, while the recurrent lobe is large and flat, and lies along the lateral and ventral surfaces of the thorax enfolded by oostegites 2–5 (Fig. 1). According to Giard & Bonnier (1887) the function of the first pair of oostegites is to agitate the contents of the brood chamber, and to prevent the eggs and embryos being crushed. However as the oostegites are more or less immobile, the latter is probably their principal use. There is a blood vessel, the marginal sinus (*ms*), which emerges from the base of the oostegite and passes around the free borders of all three lobes. On the ascendant lobe there is a median vessel (*mv*) which joins the marginal sinus distally. There are two branching blood vessels on the lateral lobe, and one median vessel on the recurrent lobe which sends branches towards the marginal sinus (Fig. 2). The ascendant lobe is stiffened by a clear firm rod which runs alongside the median vessel (Fig. 2, *sr*). The other oostegites are without prominent blood vessels or stiffening supports.

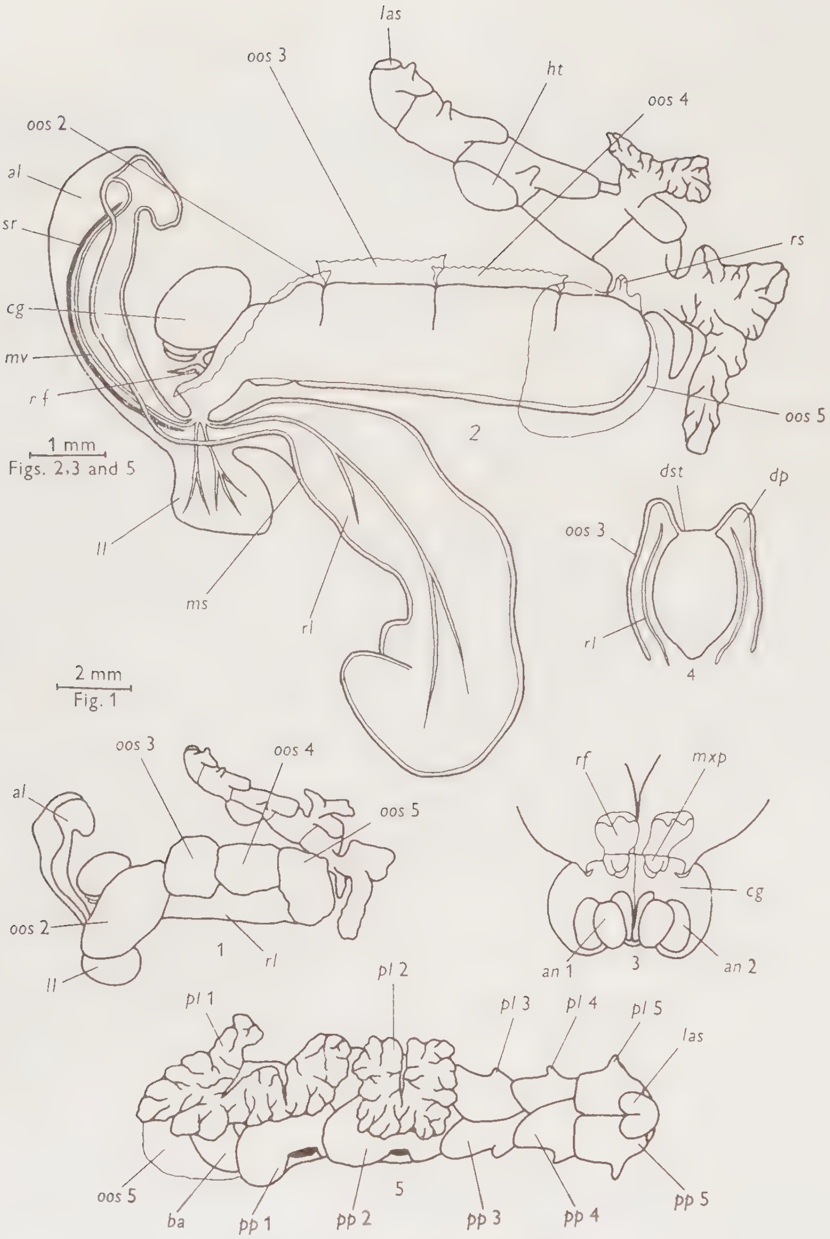
Oostegite 2 encloses the base of oostegite 1, and oostegites 3–5 enclose the rest of the thorax, overlapping to form the brood chamber (Fig. 1). They extend dorsally before being reflexed ventrally, and thus form dorsal pouches (Fig. 4). Their margins are slightly irregular, but are nowhere strongly dissected. In the angle between the thorax and abdomen the bases of the fifth oostegites are swollen and folded to form a tubular structure on each side. This may be a receptaculum seminis, such as occurs in a corresponding position in *Pinnotherion vermiforme* (Atkins, 1933). Traces of segmentation are visible on the thorax, corresponding with the oostegites.

The abdomen (Fig. 5) is sharply reflexed along the dorsal surface of the thorax, and is approximately half the diameter of the thorax. There are five segments bearing appendages, and a small sixth segment which is bifid and situated ventrally (Fig. 5, *las*). The heart (Fig. 2, *ht*) forms a hemispherical swelling on the dorsal surface of the third segment. Each of the five appendage-bearing segments has ventrally a pair of lamellae, which are the uniramous pleopods. They overlap the lamellae of the preceding segment, and in segments 1–4 one of the pair overlaps the other medially, without, however, showing a regular pattern of imbrication in the three specimens examined. Another series of structures, the pleural lamellae, arises from the bases of the pleopods. In segments one and two they are complex convoluted lamellae, and in segments 3–5 they are simple styliform processes. Giard & Bonnier (1887) suggest that they may have a respiratory function.

The incubatory chamber was packed with round, pale orange eggs, 0·15 mm in diameter.

The two ripening females differ slightly from the above description. The segmentation of the thorax is more marked, and the oostegites are smaller, especially the first. Oostegites 3–5 do not form dorsal pouches. The ovaries contain tightly packed polygonal eggs, orange in colour, diameter 0·1 mm approximately.

The distance from the anterior end of the cephalogaster to the rear of the thorax, and the length of the abdomen, respectively, for the three female specimens were: ovigerous female—7·0, 5·0 mm; first ripening female —6·4, 4·8 mm; second ripening female —7·2, 5·4 mm.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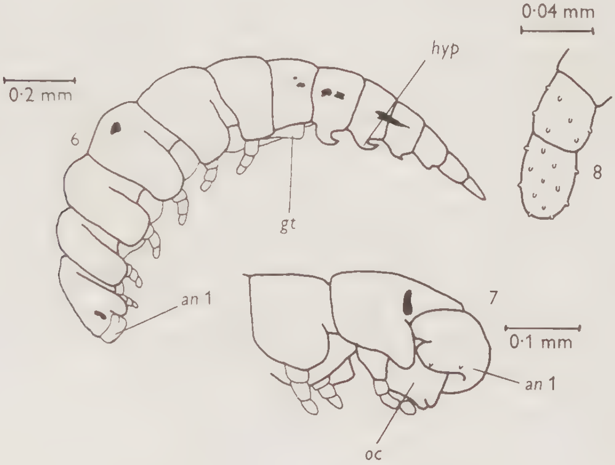
Figs. 1–5. *Entionella monensis*, female.

Fig. 1. Oostegites *in situ*.
Fig. 2. Oostegites 2, 3 and 4 cut off at base.
Fig. 3. Cephalogaster ventral view.
Fig. 4. Diagrammatic transverse section at region of third oostegite.
Fig. 5. Abdomen, ventral view.

Abbreviations: *al*, ascendant lobe of first oostegite; *an* 1–2, antennae 1–2; *ba*, base of abdomen; *cg*, cephalogaster; *dp*, dorsal pouch; *dst*, dorsal surface of thorax; *ht*, heart; *las*, last abdominal segment; *ll*, lateral lobe of first oostegite; *ms*, marginal sinus; *mv*, median vessel; *mxp*, maxillipede; *oos* 1–5, oostegites 1–5; *pl* 1–5, pleural lamellae 1–5; *pp* 1–5, pleopods 1–5; *rf*, respiratory folds; *rl*, recurrent lobe of first oostegite; *rs*, receptaculum seminis; *sr*, stiffening rod.

Male (Fig. 6). Only one specimen has been found, which occurred in the visceral cavity of the crab, separated from the female by the host membrane. This may be the normal position, for Atkins (1933) found that in *Pinnotherion vermiforme* all the males discovered occurred free in the body cavity of the host. In other species of entoniscid the male occurs within the incubatory chamber or on the surface of the female.

The total length is 1·65 mm. The general colour is pale, but the hepatopancreas gives an orange colour to the posterior thoracic and anterior abdominal segments, and there are several scattered brown chromatophores.



Figs. 6–8. *Entionella monensis*, male.
Fig. 6. Lateral view.
Fig. 7. Head.
Fig. 8. Fourth peraeopod.

Abbreviations: *an* 1, first antenna; *gt*, genital tubercle; *hyp*, hyposphenians; *oc*, oral cone.

The head is blunt, and has a curved boss around its anterior margin. This is formed of the enlarged first antennae (*an* 1), which in most other species are swellings on either side of the anterior of the head. The second antennae are absent, as in *Entionella okayamaensis* Shiino. Ventrally there is a suctorial oral cone which encloses the mandibles; it has no scale-like projections on the lower lip. No maxillae or maxillipedes could be found.

The thorax has six free segments, the third to the eighth, the first and second being fused with the head. The terga of segments 2–7 are produced laterally as broad flat processes. There are six pairs of peraeopods, on segments 2–7, segment 8 lacking appendages but bearing a pair of lateral genital tubercles. The posterior peraeopods are slightly larger than the anterior ones, and all are of three segments, the terminal one rounded. The two distal segments bear a number of small blunt tubercles (Fig. 8).

The first four abdominal segments have mid-ventral projections or hyposphenians ('crochets ventraux médians', Giard & Bonnier, 1887), those on segments one and two being strongly hooked (*hyp*). The last segment, the sixth plus the telson, is pointed and unforked.

Type specimens have been deposited at the British Museum (Nat. Hist.). The ovigerous female has been selected as the holotype (register no. 1959.vi.22.1) and the male as an allotype (register no. 1959.vi.22.2).

Relation with host

The female lies within the visceral cavity of the host, separated from the viscera by a closely fitting transparent membrane of host origin. The abdomen is flexed to lie along the dorsal surface of the thorax (Fig. 2), and the cephalogaster and anus lie anteriorly in the crab. The transparent sheath opens to the branchial cavity of the host through the membranous wall dorsal to the bases of the anterior gills. The aperture is oval, major diameter 0·35–0·5 mm, and is surrounded by a thickened brown chitinous ring. In the crab cotaining two female parasites there was one opening on each side. Most of the body cavity is occupied, and in the host the hepatopancreas is reduced, the male genital ducts are thin and thread like, and the gut may be displaced to one side.

The male parasite was lying midway along the dorsal surface of the thorax of the female, but separated from it by the transparent membrane, and so actually in the body cavity of the host.

The infected male crabs showed the typical external effects of parasitic castration. The chelae were shorter and the abdomen was broader, approaching the form of the normal female. This is shown in Table 1.

TABLE 1. A COMPARISON OF INFECTED MALE CRABS WITH NORMAL MALES AND FEMALES

Sex and condition of crab	Carapace length (mm)	Chelar propodus length (mm)	Ratio: carapace L. / propodus L.	Width of A.S. 4 (mm)	Ratio: carapace L. / width of A.S. 4
Parasitized male	17·5	6·6	2·65	2·55	6·86
Parasitized male	16·5	6·4	2·56	2·20	7·50
Normal male	16·5	10·4	1·59	1·55	10·64
Normal male	18·0	12·2	1·47	1·65	10·90
Normal female	16·0	5·4	2·96	3·85	4·16
Normal female	17·0	6·0	2·83	4·10	4·15

DISCUSSION

Entionella monensis sp.nov. is included in the genus *Entionella* because the female has no ovarian processes, and there are folded pleural lamellae only on the first two abdominal segments. The three species of the genus may be distinguished by means of Table 2 (partly based on that of Shiino, 1954).

E. fluviatilis and *E. okayamaensis* both occur in Japan, in hosts spending part of their life in fresh and brackish water. The discovery of *E. monensis* extends the range of the genus to European waters. There are four other genera which also occur in both of these areas: *Entoniscus* Müller, *Pinnotherion* Giard & Bonnier, *Portunion* Giard & Bonnier and *Cancrion* Giard & Bonnier.

TABLE 2. CHARACTERS SEPARATING THE SPECIES OF THE GENUS *ENTIONELLA*

		E. fluviatilis	*E. okayamaensis*	*E. monensis*
Female	Oostegite 1	All three lobes folded	Recurrent lobe not folded; many secondary pockets	Recurrent lobe not folded; no secondary pockets
	Pleural lamella 1	No stalk	Long stalk	No stalk
	Pleural lamellae 3–5	Distinct	Indistinct	Distinct
Male	Last abdominal segment	Deeply bifid	Shallowly bifid	Undivided
	Thoracic segment 8	No expansion	Lateral expansions	Lateral expansions
	Thoracic segment 2	Not fused with cephalon	Fused with cephalon	Fused with cephalon

SUMMARY

The relationships of the Entoniscidae to the other families of the Bopyrinae are briefly discussed. The nature of the parasitism of the family is considered. The characters of the genus *Entionella* are given, and a new species, *E. monensis* is described (mature female and mature male). Its relations with the host, the spider crab *Eurynome aspera*, are described. A table is provided to separate the species of the genus *Entionella*.

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HISTOLOGY OF THE LIGHT ORGANS OF *PHOLAS DACTYLUS* (LAMELLIBRANCHIA)

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(Plate 1 and Text-fig. 1)

The piddock, *Pholas dactylus* L., gives off a luminous secretion when irritated. The luminous glands which produce the secretion are two longitudinal stripes in the exhalant siphon, a pair of triangular organs in the mantle cavity near the base of the siphon, and a stripe around the ventral rim of the mantle (Panceri, 1872).

The histology of the light-organs has been described several times. A light-organ is covered by a simple columnar ciliated epithelium, below which are many glandular cells, which discharge through the surface epithelium. The outer part of the glandular layer consists of a mass of large mucus cells. Deeper lies a second glandular region containing large cells with long necks that extend to the external epithelial surface. Dubois (1892, 1914, 1928) believed that the photogenic tissue was made up of two kinds of secretory cells; these were the superficial ciliated cells, which possessed glandular bases (fixed secretory cells); and deeper lying glandular cells derived from clasmatocytes (migratory secretory cells). Rawitz (1891) clearly distinguished a mucous from an underlying photogenic layer. The latter, according to Förster (1914), contains pyriform cells with long necks. He believed that he could distinguish a secretory cycle in the photogenic cells. Exhausted cells at the beginning of the cycle possessed an alveolar cytoplasm; granules began to appear in the cytoplasm; the granules increased in number and stained intensely with iron haematoxylin. Those photogenic cells which were filled with granules were in the active secretory state. Transitional stages between the inactive (or depleted) cells and the active (granular) cells were rare. An account by Dahlgren (1916) is based on the work of Förster (1914).

While examining some sections of the light-organs of *Pholas*, I made certain observations which differed from the published accounts. Moreover, the latter were difficult to reconcile with one another. Therefore, I undertook the following study of the light-organs of *Pholas dactylus*.

METHODS

The triangular organs and the siphonal cords were excised together with a little contiguous tissue. The material was fixed in Zenker's fluid, and cut in polyester wax (Steedman, 1957). Stains used were: thionin; Alcian blue and neutral red; mucicarmine; Giemsa; Masson's trichrome stain; van Gieson's stain; a modification of Masson's, consisting of Weigert's haematoxylin, aniline blue and xylidine ponceau; iron haematoxylin; Ehrlich's haematoxylin and eosin.

OBSERVATIONS

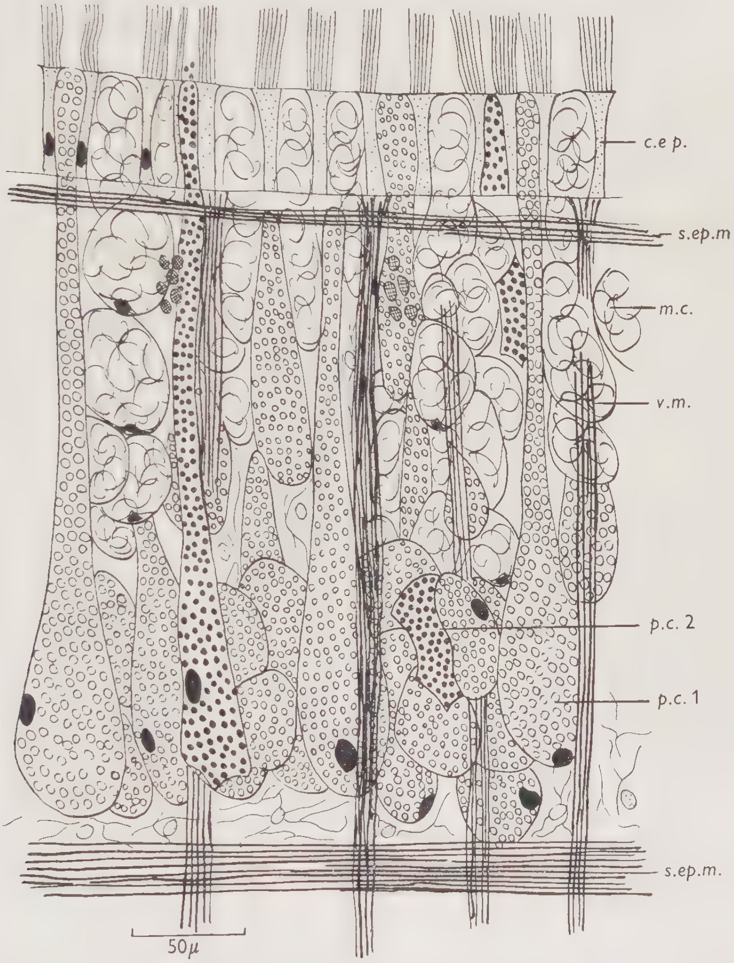
The general histological picture described by earlier workers is confirmed (Text-fig. 1; Pl. I). The epithelium overlying the light-organ, as elsewhere, contains ciliated columnar cells. Between them open the distal extremities of the underlying glandular cells. In vertical section, the ciliated epithelial cells expand externally into cones, which arch over the necks of the glandular cells. Underneath the epithelium is a thick and dense layer of mucus cells, some 180 μ deep, which extend down to and into the outer part of the photogenic layer (Text-fig. 1; Pl. I). These mucus cells are large, up to 180 μ long and about 13 μ wide at the base. They open by fairly wide necks, 6–7 μ across, between the epithelial cells. Except for their very large size, these cells are typical mucus cells. Their staining affinities are listed in Table 1. With some stains they are coloured much more intensely than the ordinary mucus goblet cells occurring elsewhere in the epithelium.

Below the mucus cells there is another dense glandular layer. This, the photogenic tissue, consists of closely packed secretory cells. They occupy a layer approximately 120 μ thick, beginning about 160 μ from the surface. Thus, the mucus layer and the photogenic layer overlap to some extent.

Two kinds of cells can be distinguished in the photogenic layer by their staining affinities (see Table 1). Let these cells be known as types 1 and 2 (Text-fig. 1). Both types of cells have granular contents. Photogenic cells of type 1 are more abundant (Text-fig. 1; Pl. I). The granules are basophilic to some plasma stains: they stain weakly with iron haematoxylin and eosin, red with mucicarmine, green with light green, etc. Cells of type 2 are infrequent, relative to type 1. Their coarse granules are acidophilic; they stain red with eosin, neutral red and xylidine ponceau, and possess stronger affinity for iron haematoxylin.

Photogenic cells, type 1 (Text-fig. 1). These are packed closely together, up to 270 μ long and 15 μ wide at the base. They have the shape of long pyriform sacs with long necks, 4–5 μ wide, extending to the epithelial surface. The small nucleus lies basally, either in the lateral wall or at the bottom of the cell. The interior of the cell is packed with coarse granules, having an average diameter of about 1·3 μ. The cell is invested by a thin cytoplasmic sheath staining with xylidine ponceau. The secretory granules extend through the necks of the cells to the external surface; discharged to the exterior, they lose their identity. A homogeneous flocculent precipitate lies over the external surface of the epithelium.

Photogenic cells, type 2 (Text-fig. 1). These have about the same dimensions as cell type 1. They extend well down into the photogenic layer. At the base they are about 11 μ wide; the necks are 4·5 μ wide where they pass through the epithelial layer. A small nucleus lies against the wall of the cell in the basal region. The interior of the cell is packed with coarse spherical granules, having an average diameter of about 1·1 μ. They extend up to the external epithelium, where they can be seen emerging from the mouths of the cells. The cytoplasmic wall is difficult to distinguish.



Text-fig. 1. Semi-diagrammatic representation of the triangular light-organ of *Pholas dactylus*, from vertical sections. Legend: *c.ep.*, ciliated epithelium; *m.c.*, mucus cell; *p.c.* 1., photogenic cell type 1; *p.c.* 2, photogenic cell type 2; *s.ep.m.*, subepithelial muscle; *v.m.*, vertical muscle.

Previous workers (Dubois, 1892, 1914; Förster, 1914) have laid much emphasis on the muscle system in the vicinity of the light-organ. The following description is based on the siphonal cord (Text-fig. 1; Pl. I), but the arrangement is similar in the triangular organ. There is a subepithelial muscle consisting of three layers lying parallel to the surface. These are (from the external surface, inwards), transverse, longitudinal and transverse (or circular). The last (and innermost) layer is thicker than the others, and descends underneath the light-organ. Underneath the last-mentioned muscle are thick bundles of strongly developed longitudinal muscles. Vertical muscle strands run from the basement membrane below the external epithelium through the light-organ.

TABLE 1. STAINING CHARACTERISTICS OF GLANDULAR CELLS

Stains	Goblet cells of epidermis	Mucus cells of the light-organ	Basal cells type 1 of light-organ	Basal cells type 2 of light-organ
Thionin	Unstained or purple	Purple	Blue	Darker blue
Alcian blue and neutral red	Light blue	Blue	Blue	Red
Mucicarmine	Unstained	Red	Red	Unstained
Giemsa	Purple	Purple	Blue	Blue
Masson's	Unstained or very faint green	Unstained or very faint green	Green	Red
Van Gieson's	Unstained	Unstained	Yellow	Yellow
Weigert's haematoxylin, aniline blue, xylidine ponceau	Unstained or very light blue	Unstained	Blue	Red
Haematoxylin and eosin + Biebrich scarlet	Faint blue	Blue	Faint pink	Red
Methyl blue and eosin	Unstained	Unstained	Predominantly blue	Red
Iron haematoxylin	Unstained	Unstained	Grey—faintly stained	Black

DISCUSSION AND CONCLUSIONS

The outer glandular layer clearly consists of mucus cells. These have the staining affinities discovered by Förster (1914), viz. metachromatism with thionin, affinity for mucicarmine, and the additional staining features listed in Table 1. They are enormous relative to the goblet cells of the surface epithelium elsewhere. Moreover, there are differences in the staining affinities of these two types of mucus cells, since the mucinogen of the ordinary goblet cells stains poorly or not at all with thionin and mucicarmine. Possibly, different types of mucins are produced by goblet cells of the epithelium and mucus cells of the light-organ. Certainly, the large size and numerical abundance of these cells in the light-organs indicate that they are concerned with photogeny, and their functional role may be to produce a mucin-carrier for the photogenic secretion.

There are two kinds of secretory cells in the lower glandular or photogenic layer. Both types of cells are filled with granular inclusions which differ in staining affinities. As a generalization, the granules of cell type 1 have rather poor staining affinities; those of cell type 2 are acidophilic and have strong staining affinities. The staining characteristics allow the two kinds of cells to be distinguished clearly from each other. Cells of both types can be seen discharging through the external epithelium.

Förster's interpretation of a transformation in the photogenic cells from an alveolar to a granular condition seems to be based on failure to distinguish two kinds of secretory cells in the inner glandular or photogenic layer. Dahlgren (1916) accepted Förster's account, and his artist clearly illustrated two kinds of cells in the photogenic layer, viz. alveolar cells with a coarse meshwork and cells with darkly staining small granules. The latter, presumably, were stained with iron haematoxylin (cf. elsewhere in Dahlgren's work). The alveoli appear to be unstained granules of cell type 1, and are grossly exaggerated in size. A most interesting feature of Dahlgren's illustration is that the alveolar cells (photogenic cells, type 1) are shown discharging at the surface; granules of the other kind of cell (photogenic cells, type 2) are shown as extending along the neck of the cell to the external surface.

Förster (1914) considered that the outer glandular layer (of mucus cells) was concerned solely with the production of mucus. Dubois (1892, 1914) demonstrated the basic luciferin-luciferase reaction in the secretion of *Pholas* (cf. Harvey, 1957). Dahlgren (1916), without evidence, assigned luciferin to granular cells of the inner glandular (i.e. photogenic) layer, luciferase to the outer glandular (i.e. mucus) layer. Since there are two kinds of secretory cells in the photogenic layer, it is logical to link them with the production of luciferin and luciferase; possibly, the luciferase corresponds to the eosinophilic granules of less abundant cell type 2. This is mere speculation, however.

Previous authors (Dubois, 1914; Förster, 1914) have assumed that the luminous secretion of *Pholas* is discharged by muscular contraction. The luminous gland cells of *Pholas* much resemble those of *Chaetopterus*. The latter discharges a luminous secretion from unicellular glands, and its photogenic tissue lacks muscle fibres. In both animals the luminescence is under nervous control; the gland cells are filled with granules, and these emerge through an open pore at the apex of the cell. Instead of invoking a muscular mechanism, I would suggest that the walls of these cells consist of oriented contractile protein capable of expressing the cell contents. A model may be found in the contractile behaviour of monolayers of actomyosin (Bennett, 1956; Giese, 1957).

I am grateful to Mr A. C. G. Best for the excellent histological preparations and for the photography.

SUMMARY

Earlier work dealing with the histology of the light-organs of *Pholas dactylus* is reviewed.

Beneath the surface epithelium of the light-organ, two glandular layers can be distinguished. One, an outer glandular layer, contains mucus cells. The other, an inner layer, contains two kinds of granular cells, which can be separated by their staining characteristics. The latter are listed in Table 1. Both kinds of granular cells of the inner layer discharge their contents upon the external surface. The photogenic secretions are produced, most probably, by the glandular cells of the inner layer.

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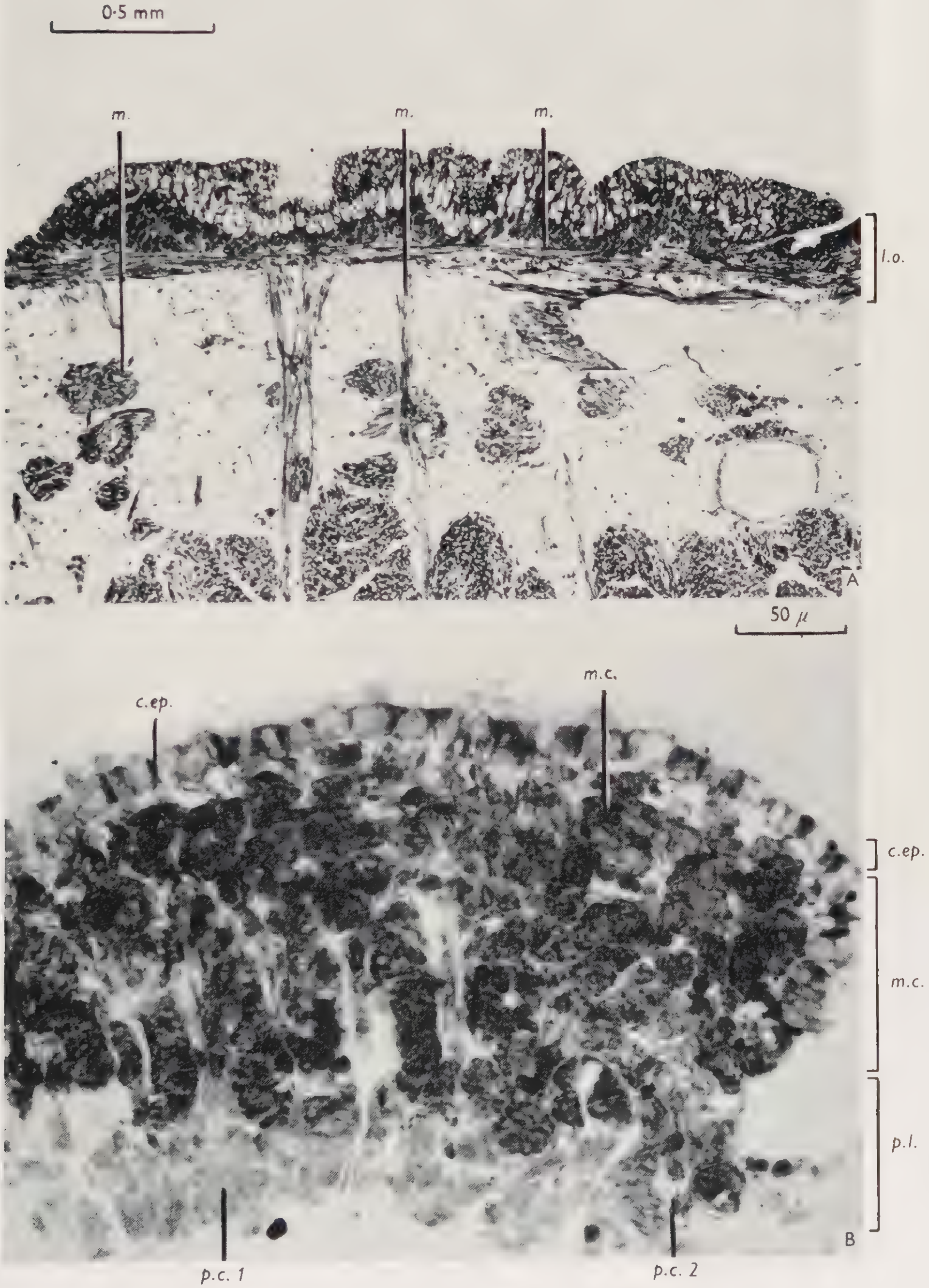
EXPLANATION OF PLATE I

Plate I. A. General view of a triangular light organ of *Pholas dactylus*. Iron haematoxylin, acid fuchsin-ponceau 2R, aniline blue. Mucus cells unstained; photogenic cells dark. B. View of siphonal light-organ, showing mucus cells. Giemsa. Legend: *l.o.*, light organ. *m.*, muscle. *c.ep.*, ciliated epithelium. *m.c.*, mucus cells. *p.c.* 1, *p.c.* 2, photogenic cells, types 1 and 2, respectively. *p.l.*, photogenic layer. Mucus cells dark; photogenic cells, type 1, light; photogenic cells, type 2, with dark granules.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DEFENSIVE ACID-SECRETION IN MARINE GASTROPODS

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(Text-fig. 1)

An important function of the gastropod shell is to protect the body against attack by predators. If the shell of a whelk is broken away and the soft animal is then offered to a hungry cod, it is eaten readily. Many successful gastropods, however, lack an external shell as adults (although it is certain that all have evolved from shelled ancestors) and might be expected to be eaten by fish as readily as is the naked body of a broken whelk. The purpose of this paper is to describe part of an investigation into whether this is in fact true.

Some authors have considered that many of these naked gastropods (the majority of which belong to the Opisthobranchia) escape being eaten by their cryptic coloration and their habit of 'skulking under stones or in crannies' (Crossland, 1911, p. 1063). Some have considered that many opisthobranchs are distasteful in various ways and believed the behaviour and coloration of such forms to be 'warning' in nature. Thus it might be expected that, under experimental conditions, cryptically coloured opisthobranchs would be accepted as food by fish while the more vividly coloured ones would be rejected, for the usual line of reasoning indicates that aposematic or warning coloration and behaviour accompany the possession of some defensive mechanism, while cryptic coloration and habits usually characterize animals which would be quickly killed and eaten if plainly visible to their enemies. Few experiments have been done with opisthobranchs. Herdman & Clubb (1892) describe some interesting experiments with marine aquarium fish and nudibranchs, but these were inconclusive since only a very few species of the latter were used. Crossland (1911) established that fish refused live chromodorid nudibranchs thrown to them from a boat in shallow water, while readily accepting other food and even taking formalin-soaked oysters. Many workers tended to be over-subjective and were handicapped by disagreements, often resulting from the description of animals removed from their natural surroundings. For instance, Crossland (1911, p. 1064) states that 'Tritonids ...are fairly conspicuously coloured', while most other authorities would agree that tritoniids resemble closely the alcyonarians on which they live and feed. Similarly, Cooke (1895, p. 73) states that *Pleurobranchus membranaceus* is 'conspicuously marked with red-brown and yellowish "warning" colours. *Haminoea* and *Philine*, on the other hand, are good to eat, and consequently possess "protective" coloration'; these statements are based on faulty knowledge of these opisthobranchs.

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It is clear that a full re-examination of the subject is necessary. To this end, I have made observations on as wide a variety of naked gastropods as possible, attempting to relate the results obtained to the facts of their natural history and anatomical and histological structure. The present paper describes the results of a part of this work, dealing with some gastropods which proved to rely on the production of an acid fluid for the deterrence of would-be predators. That *Pleurobranchus membranaceus* was able to secrete an acid substance has been known for many years (Garstang, 1890). Other species of gastropods now found to do this are: *Berthella plumula* (Opisthobranchia:Pleurobranchidae); *Philine quadripartita* (Opisthobranchia:Philinidae); *Lamellaria perspicua* (Prosobranchia:Lamellariidae); *Velutina velutina* (Prosobranchia: Lamellariidae). *Velutina* is not truly naked but observations on it are included here for it raises some interesting points. Some observations on *Pleurobranchus* are given by Thompson & Slinn (1959).

The classification and nomenclature employed herein are those advocated by the Port Erin Fauna list (to be published).

METHODS

In the feeding-acceptability tests the fish used were in glass-fronted tanks in the Port Erin Aquarium, illuminated artificially, and usually fed twice per week with chopped herring or boiled mussels. Experiments were always carried out when the fish were to be expected to be hungry and this was confirmed by giving them some of their usual food before and after the experiments. The gastropod to be tested was dropped into the tank from above and allowed to sink to the bottom; the responses of the various fish were noted. Particular care was taken to ensure that the gastropods to be used in the tests were not damaged or in any way feeble, for previous experience had shown that, when vitality is low, resistance to predators may fall. It is admitted that the results of such tests must be interpreted with caution for a variety of reasons; the reliability of the results obtained will be discussed below.

Material for sectioning was fixed in Zenker's fluid (with or without acetic acid) or Lewitsky's fluid with sodium chloride added, cleared with amyl acetate and embedded in Hance's rubber wax (Gurr). Sections were cut at 4 and 6 μ. The stains employed were either the azan or the alum haematoxylin of Heidenhain, with, as counterstains for the latter, eosin and alcian blue 8GS (Steedman, 1950). In addition, preparations stained intravitally with neutral red were useful.

RESULTS OF ACCEPTABILITY TESTS

Tests with fish

Some tests carried out using *Pleurobranchus membranaceus* have been described by Thompson & Slinn (1959). In the present investigation further experiments with this species have yielded confirmatory data.

With *Philine quadripartita*, *Lamellaria perspicua* and *Berthella plumula*, essentially similar results were obtained in the present study. No tests were carried out using *Velutina velutina*, for only one live specimen was available and this was required for study of the histology of the foot.

Fish used in the tests were *Blennius pholis*, *Acanthocottus bubalis*, *Pholis gunnellus*, *Pleuronectes platessa*, *Spinachia spinachia*, *Gadus morrhua*, *Pollachius pollachius* and *P. virens*. (Tests with *Agonus cataphractus* and *Ciliata mustelas* were unsatisfactory for these fish invariably ignored test organisms.) The usual reaction to the test animal was for the fish to inspect it closely; the height in the tank at which the fish became aware of the mollusc and the means of inspection (olfactory or optical) varied with the different species of fish. Occasionally a fish would take one of the test molluscs into its mouth, but invariably rejected it violently and immediately. In a tank containing several pollack (*Pollachius pollachius*) a single test mollusc may be inspected, taken into the mouth and rejected by every fish present before it reaches the tank bottom. No evidence that any of the fish 'learned' to ignore these molluscs was obtained. There is little point in describing in detail the reactions of the various species of fish employed, for the behaviour of fish with regard to test foods has been described particularly fully by Bateson (1890).

To summarize: none of the four species of gastropod used was ever seen to be ingested by any of the fish employed; occasionally the fish would 'taste' the mollusc but always rejected it. The following observations are relevant to the contention that the tests yielded reliable data, and reflect the probable behaviour of these fish when encountering these molluscs in nature: (*a*) in nature, large numbers of swimming *Pleurobranchus* were ignored by shoals of coalfish (*P. virens*) (Thompson & Slinn, 1959); (*b*) a detailed study of the gut contents of gadoid fish from the seas around the south of the Isle of Man (personal communication from A. K. Nagabhushanam) revealed none of the molluscs under consideration, except for a specimen of *Velutina velutina* from the stomach of a coalfish, *P. virens*, in December 1956).

Tests with anemones

Thompson & Slinn (1959) state that *Tealia felina* rejected live *Pleurobranchus* in laboratory tests. This has been confirmed and found to apply also to *Berthella plumula*, but with this important proviso: rejection only occurs predictably the first time the test is performed with any individual gastropod; if a rejected pleurobranchid is immediately placed in the tentacles of a fresh

Tealia, the mollusc is often ingested readily. The significance of this is difficult to estimate; escape from the first anemone may have temporarily exhausted the deterrent reserves of the pleurobranchid.

ACID SECRETION

If the molluscs under consideration are roughly stimulated with a glass rod and a pH paper is applied, it can be seen that a strongly acid secretion has been produced. The pH estimations were made with B.D.H. wide-range papers; the colour change indicated the acidity of the secretion to be approximately pH 1. The secretion is not produced continuously but only after a disturbance; pH papers resting lightly upon the animal while it is creeping exhibit no colour change.

Thompson & Slinn (1959) found that the nature of this acid secretion in *Pleurobranchus* was relatively simple; it may be considered to be a mixture of sulphuric and hydrochloric acids, the former predominating. No organic acid radicals were identified nor were proteins present in appreciable amounts. The proportion of sulphate to chloride was much higher in the secretion than in either sea water or molluscan blood (Robertson, 1949).

In *Pleurobranchus*, *Berthella*, *Philine* and *Lamellaria* the acid secretion was produced at any point on the body surface; even the gills of the two pleurobranchid species are able to secrete this acid if disturbed. In *Velutina* the foot certainly was able to produce acid, but it is not certain whether in addition the mantle has this capacity.

ACID-SECRETING TISSUES

Pleurobranchus membranaceus

Thompson & Slinn (1959) describe the histology of the mantle and foot epidermis. The 'empty' appearance of the epidermal cells is characteristic of acid-secreting tissues in the gastropods investigated. Scattered unicellular mucus glands are also present, especially in the pedal epidermis.

Sections through the gill show epidermal acid cells to be abundant. The metapodial gland (which develops as maturity is reached) has a totally different structure, packed with large compound multicellular glands of complex cytological aspect; its functions are presumably connected with adhesion to the substratum.

In sections through the mantle, cilia are never detectable (although plainly evident in life) but they are clearly demonstrable in sections through the foot.

Berthella plumula

The epidermis of *Berthella* shows only minor differences from that of *Pleurobranchus*. The contents of the acid cells in life stain red with neutral red; it is well known that this stain (for which the name 'neutral' red is misleading) can act as an indicator, red being the colour it adopts in acid media. Squashing of an excised piece of the mantle beneath a cover-glass causes the acid fluid to be released by rupture of some of the cells. The secretion at first takes the form of large spherules, one from each epidermal cell, but they soon merge and disperse through the surrounding medium.

Simple calcareous spicules are present in the subepidermal layer of the mantle. That these can exist in such close proximity to cells containing a strongly acid fluid is rather surprising; when a small piece of the mantle is compressed under a cover-glass the acid is freed and the spicules rapidly dissolve.

As in *Pleurobranchus*, cilia are not detectable in the mantle after fixation, and the metapodial gland, which develops late in life, is histologically complex and does not seem to be concerned with acid secretion.

Philine quadripartita

The whole integument is able to secrete the acid fluid. The epidermis differs markedly from that of the pleurobranchids; the acid glands are large, flask-shaped, subepidermal sacs, appearing as minute white specks in life and empty in sections. Between the sacs is a network of muscle fibres; discharge of the acid is probably brought about by the contraction of these fibres. Unicellular subepidermal mucous glands are also present, discharging to the exterior through separate ducts perforating the simple ciliated epidermis.

Lamellaria perspicua *and* Velutina velutina

As in *Philine*, the epidermis is simple and ciliated, while the acid glands take the form of subepidermal sacs communicating with the exterior by separate ducts perforating the epidermal layer. Muscle fibres are present around the sacs. The shell of *Velutina* is covered externally by a peculiar horny sheath; it seems probable that one of its functions is to protect the calcareous shell against the acid secretion of the animal's own foot. Fig. 1 illustrates diagrammatically the two types of epithelium found in acid-secreting gastropods.

DISCUSSION

All the gastropods described in this paper were found to be distasteful to fish; all are able to secrete a strongly acid fluid; all show similar glands in the skin. Strong circumstantial grounds exist for believing the glands to be in all cases the producers of the acid, and the acid to be the deterrent to the fish.

Bateson (1890) discovered that even dilute acids are repellent to a variety of fish. He states (p. 247): 'Conger are equally willing to eat a piece of squid or pilchard if it is covered or smeared with spirit, cheese of various sorts, anchovy extract, or *Balanoglossus*, as if it had been unpolluted. On the other hand, they will refuse cooked or tainted food and food which has been soaked for a few moments in dilute acids. The same remarks apply generally to the other fishes'. There can thus be little doubt that it was the acid secretion which brought about the rejection of the gastropods used in my experiments. This is further supported by the fact that dead or dying *Berthella* were eaten readily; the deterrence is essentially a living process and cannot be explained simply on the grounds that the test foods were unfamiliar to the fish.

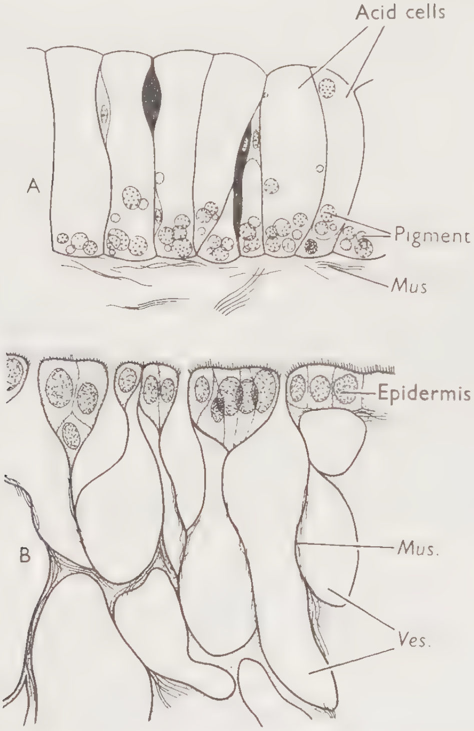

Fig. 1. Diagrams of sections through the two types of acid-secreting epithelia found in gastropods. A, characteristic of *Berthella plumula* and *Pleurobranchus membranaceus*; B, characteristic of *Philine quadripartita*, *Lamellaria perspicua* and *Velutina velutina*. Mucous glands are shown black. *Mus.*, muscle fibres. *Ves.*, empty acid vesicles.

That the acid is produced by the glands described in this paper is difficult to prove, but is supported by much indirect evidence: (1) the histological structure of the median buccal gland (acid gland) of *Pleurobranchus* (Thompson & Slinn, 1959) is remarkable for the 'empty' appearance of the cells in stained sections. Because these cells undoubtedly secrete acid, and because all the glands described in the present paper resemble them so closely, there are grounds for believing the function of all to be the same. (2) Excised pieces of the mantle skirt of *Berthella* can secrete acid; this rules out any possibility that the fluid might reach the exterior by seepage from the median buccal gland of the pleurobranchids. (3) Preparations of small excised pieces of the mantle of *Berthella* showed that rupture of the epidermal cells and liberation of the contained fluid (which neutral red staining showed to be acidic) was followed closely by the solution of the subepidermal calcareous spicules. This is proof of the acid-secreting function of the 'empty' epidermal cells of *Berthella*, and provides further grounds for believing, by analogy, the glands of the other species to have the same function.

Thus we may suppose that: (*a*) large distinctive glands are present in the skin of the five species dealt with; (*b*) when the animal is disturbed acid is discharged by these glands; (*c*) this acid secretion will usually cause the rejection of the mollusc by any fish which attempts to ingest it.

None of the five species is vividly coloured, notwithstanding Cooke's (1895) opinion that *Pleurobranchus* shows warning coloration. All, from *Philine* which lives submerged beneath sand or mud (Brown, 1934) to *Lamellaria*, which may bury itself in the ascidians on which it feeds (Herdman, 1893), are fairly effectively camouflaged. None shows any warning coloration or behaviour.

Acid secretion must have arisen independently in the Pleurobranchidae, the Philinidae and the Lamellariidae, which are distinct, well-defined taxonomic groups. This independent evolution of a similar defence mechanism in three groups of gastropods makes it all the more interesting that, while two of the groups (Philinidae and Lamellariidae) have evolved subepidermal acid glands (Fig. 1 B), the third (Pleurobranchidae) makes use of the epidermal cells for the purpose (Fig. 1 A). Perhaps the former condition was derived from an epithelium similar to that of modern pleurobranchids.

Although a considerable number of British gastropods have been tested during the present investigation, many more species undoubtedly would prove to have acid glands, if more naturalists were aware of the possibility of their existence. It is to be hoped that workers with the necessary skill will interest themselves in the chemical nature of these acid secretions; it would be of particular interest to know whether essentially the same acids are produced by the various groups. Furthermore, the functioning of the epidermal cilia in animals whose external pH may vary from 1 to 7 within a few seconds deserves further attention.

The author is indebted to Mr J. S. Colman for critical reading of the manuscript and for the provision of laboratory facilities. In addition it is a pleasure to acknowledge the assistance given by Mr R. G. Hartnoll, Mr D. Eggleston and Mr P. J. Miller in collecting the material on which this paper is based. The work was done while the author was holder of a Leverhulme Fellowship in the University of Liverpool.

SUMMARY

The ability, on being abruptly disturbed, to secrete through the skin strongly acid fluids (approximately pH 1) is recorded for five species of British gastropod molluscs. These are the prosobranchs *Lamellaria perspicua* and *Velutina velutina* and the opisthobranchs *Philine quadripartita*, *Berthella plumula* and *Pleurobranchus membranaceus*. All but *Velutina* lack an external shell as adults.

The tissue responsible for the acid secretions presents a characteristically 'empty' appearance in histological preparations. In *Lamellaria*, *Velutina* and *Philine* the acid glands take the form of subepidermal sacs communicating with the exterior through separate ducts perforating the simple ciliated epidermal layer. In *Berthella* and *Pleurobranchus* the secretion is elaborated within the ciliated epidermal cells themselves.

The ability to secrete acid fluids through the skin appears to have arisen independently at least three times, for the three families concerned in this study (Pleurobranchidae, Philinidae and Lamellariidae) are not closely related.

Tests in large aquaria led to the conclusion that the above-mentioned gastropods are invariably rejected as food by a variety of species of fish. After a consideration of the reliability of such tests, it is concluded that it is in fact the acid-secretion mechanism of the gastropod which is responsible for the deterrence of predatorial fish.

It is suggested that the ability to secrete acids through the skin may be a widespread phenomenon among gastropods.

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DEFENSIVE ADAPTATIONS IN OPISTHOBRANCHS

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(Text-fig. 1)

This is the third and concluding part of an investigation into defensive mechanisms in some British gastropods. The first part (Thompson & Slinn, 1959) dealt with a single species of opisthobranch, *Pleurobranchus membranaceus*, which proved able to secrete a strong acid if disturbed. The second part (Thompson, 1960*a*) recorded further instances of acid secretion. The present paper describes the remainder of my work on opisthobranchs.

The two earlier studies were rendered more easy to interpret by the relatively simple nature of the defensive fluid; in the forms to be dealt with herein it has not been possible to attempt any biochemical investigations in view of the complexity and diversity of the materials involved.

Observations on defensive adaptations in opisthobranchs were made by Garstang (1889, 1890*a*), by Herdman & Clubb (1892), by Crossland (1911) and by Crozier (1917). Cott (1940), in *Adaptive Coloration in Animals*, summarizes the work of Garstang and Crossland, but omits any reference in the text to that of Crozier or of Herdman & Clubb. It is unfortunate that Cott's account is marred by some misconceptions regarding opisthobranchs; for instance, after mentioning the batteries of nematocysts possessed by some nudibranchs, he states (p. 254) in a section entitled 'Poison in defence': 'So effective are these batteries as a deterrent, that fishes have been known to eat shelled molluscs such as *Margaritifera* which had been long pickled in formalin, in preference to fresh specimens of the Nudibranch *Chromodoris*.' Chromodorid nudibranchs do not possess nematocysts. Similarly, in a section entitled 'Warning coloration in other groups of animals', Cott mentions Garstang's (1890*a*) work as follows: 'Certain species in the suborder [Tectibranchia], such as *Scaphander lignarius*, *Haminoea hydatis*, and *Philine aperta*, are largely preyed upon by fishes and are inconspicuously coloured. On the other hand, the related *Oscanius membranaceus*, a form rendered highly distasteful by defensive acid secretions, "is not eaten by fishes, and is handsomely coloured with red-brown and yellowish markings"' (Cott, 1940, p. 270). It has already been pointed out (Thompson & Slinn, 1959) that *Pleurobranchus* (= *Oscanius*) *membranaceus* does not exhibit warning coloration; that *Philine* can secrete a fluid of the same acidity (approximately pH 1—see Thompson, 1960*a*) as that of *Pleurobranchus*; and, furthermore, I know of no evidence that *Scaphander*, *Philine* and *Haminoea* are 'largely preyed upon' by fish (see the discussion to the present paper). Cott's arguments here are based on faulty knowledge of the opisthobranchs concerned.

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It was clear that a re-investigation of the subject of defence in opisthobranchs was necessary; to this end, I have made observations on as wide a variety of forms as possible, attempting to relate the morphology and natural history of the mollusc to data resulting from aquarium experiments with fish.

The nomenclature and classification of British animals mentioned herein are those advocated by the Port Erin Fauna list (to be published). In the case of foreign species, the name employed is that used by the author cited.

METHODS

Material for sectioning was fixed in the fluids of Zenker (with or without acetic acid), Helly, Perényi, Bouin, Lewitsky (with added sodium chloride) or Ciaccio. Of these, the last two gave by far the best results. The embedding medium used was Hance's rubber wax (Gurr) and sections were cut at from 4 to 10 μ. Stains employed included the azan and the alum haematoxylin of Heidenhain, safranin and light green, Mayer's haemalum, eosin and alcian blue 8GS (Steedman, 1950). Preparations stained intravitally with neutral red were useful.

In the feeding-acceptability experiments, the procedure and the species of fish used were exactly as described in an earlier paper (Thompson, 1960*a*). These experiments were carried out in the Port Erin Aquarium. Each species of opisthobranch was tested at least twelve times; with the more readily obtainable species of nudibranch, the number of tests made was nearer thirty. Because of the difference in size between the various species of opisthobranchs, the fish to which any individual mollusc was offered was selected partly on the grounds of its size; there would have been little point, for instance, in offering the tiny *Elysia* or *Doto* to a large cod, for such fish often ignore very small objects. Particular care was taken always to ensure that the opisthobranchs tested were not damaged or otherwise enfeebled, for experience showed that resistance to enemies falls if vitality is low.

To test the taste of various opisthobranchs to the human palate, the specimens were first rubbed between the fingers in order to initiate any defensive reaction, and then placed in the mouth; the reactions of the observer were recorded. The results of these tests were not uniformly reliable for difficulty was experienced in separating the saline taste of the medium from the taste of any defensive secretion; it is probable that the human tongue fails to detect some of these secretions, especially in the case of the smallest molluscs. The tests were carried out by the author and Mr D. Eggleston.

The acidity of the skin secretions was estimated by means of B.D.H. pH papers.

RESULTS

Feeding-acceptability tests

The results of the aquarium tests were rather uniform. No healthy opisthobranch (with a solitary exception) was ever seen to be ingested by any of the fish used. The exception was a single *Hero formosa* which was eaten by an *Acanthocottus*, while other individuals were invariably rejected. Dead or severely damaged opisthobranchs were, however, usually taken readily. The fish usually inspected the test organism closely (the manner of inspection varying with the species of fish); on some occasions a healthy opisthobranch was taken into the mouth but rejection almost invariably followed. In a large tank containing a number of excited hungry fish, a mollusc may be 'tasted' by every individual present before it reaches the bottom. The test organisms were seldom damaged in the process of tasting and rejection. There is no point in giving here any details concerning the behaviour of the fish used in these experiments, since Bateson (1890) describes particularly fully the reactions of various species of fish to test foods.

Further observations

In Table 1, data concerning the histology of the skin, natural history and defensive behaviour are listed for the species of opisthobranchs investigated. These data are derived mainly from the present investigation. For each species reference is made to a work in which appears a good illustration; in this way lengthy descriptions of the external features have been avoided. Epidermal mucous glands have been ignored; wherever the term gland is used alone, it may be taken to mean non-mucous gland.

DISCUSSION OF LITERATURE

Records of the predation of fish on bottom-living opisthobranchs are few. Of the species listed in Table 1, only *Tritonia hombergi*, *Scaphander lignarius* and *Philine quadripartita* have been found to be eaten by fish in nature. The jaws of *Tritonia hombergi* have been found occasionally by the author in the stomachs of dogfish (*Scyliorhinus canicula*) dissected by students at University College, Bangor; Ford (1921) found *Scaphander lignarius* in the stomachs of two dogfish of this same species; Todd (1903) found *Philine quadripartita* in the stomachs of a very few fish. *Aeolidia papillosa* (a British nudibranch not dealt with in the present study) was recorded by Homans & Needler (1944) from the stomachs of young haddock (*Melanogrammus aeglefinus*). *Akera bullata* has been found (Lemche, 1929) in the stomach of *Limanda limanda.*

TABLE 1. SUMMARY OF WORK ON DEFENSIVE

(1) Species	(2) Source of data	(3) Reference to good illustration	(4) pH of skin secretion	(5) Taste to tongue	(6) Tests on fish	(7) Cnido-sacs
Aplysia punctata	P	Eales, 1921; Wilson, 1937	N	Bitter†	X	Abs.
Scaphander lignarius	P	P.-F., p. 57	N	Bitter	X	Abs.
Philine quadripartita	T(2)	P.-F., p. 65	*ca.* 1	Bitter-Sour	X	Abs.
Berthella plumula	T(2)	B.Y., Pl. 18	*ca.* 1	Bitter-Sour	X	Abs.
Pleurobranchus membranaceus	T.S.	T.S.	*ca.* 1	Bitter-Sour	X	Abs.
Hermea dendritica	P, G	A.H., 3, pl. 40	—	—	—	Abs.
Elysia viridis	P	Eliot, pl. VII	N	O	X	Abs.
Duvaucelia plebeia	P	A.H., 2, pl. 3	N	—	—	Abs.
Tritonia hombergi	P	A.H., 2, pl. 2	N	Bitter‡	X	Abs.
Dendronotus frondosus	P	A.H., 3, pl. 3	N	O	X	Abs.
Doto coronata	P	A.H., 3, pl. 6	N	O	—	Abs.
Hero formosa	P	Eliot, pl. IV	N	O	*	—
Eubranchus tricolor	P	A.H., 3, pl. 34	N	O	X	Pres.
Facelina auriculata	P	A.H., 3, pl. 12, 13	N	O	X	Pres.
Archidoris pseudoargus	P	A.H., 1, pl. 3	N	O	X	Abs.
Jorunna tomentosa	P	A.H., 1, pl. 5	N	O	X	Abs.
Acanthodoris pilosa	P	A.H., 1, pl. 15	N	O	X	Abs.
Onchidoris pusilla	P	A.H., 1, pl. 13	N	O	—	Abs.
O. fusca	P	A.H., 1, pl. 11	N	O	X	Abs.
O. muricata	P	A.H., 1, pl. 9	N	O	X	Abs.
Adalaria proxima	T(1)	A.H., 1, pl. 9	N	O	—	Abs.
Goniodoris nodosa	P	A.H., 1, pl. 18	N	O	X	Abs.
Polycera quadrilineata	P	A.H., 1, pl. 22	N	O	X	Abs.
Ancula cristata	H.C.	A.H., 1, pl. 25	—	O	X	Abs.

Notes

Column (1), name of species as in *Port Erin Marine Fauna* MS.

Column (2) refers to the following sources: P, present article; T(1), Thompson, 1958; T(2), Thompson, 1960*a*; T.S., Thompson & Slinn, 1959; G, Garstang, 1890*a*; H.C., Herdman & Clubb, 1892.

Column (3) references include: B.Y., Barrett & Yonge, 1958; A.H., Alder & Hancock, 1845–55, Families 1, 2, or 3, as indicated; P.-F., Pruvot-Fol, 1954; Eliot, 1910 (supplement to Alder & Hancock); T.S., Thompson & Slinn, 1959.

Column (4): N, neutral.

Column (5), taste to human tongue: O, None.

Column (6), acceptability to fish in tests: X, always refused; * one eaten by *Acanthocottus bubalis*, others rejected.

Column (7), cnidosacs present (Pres.) or absent (Abs.).

† Both purple secretion and body.

‡ Byne (1893) states that this secretion may blister human hands.

ADAPTATIONS IN OPISTHOBRANCHS

Species	(8) Non-mucous skin glands		(9) Regions of body poor in non-mucous skin glands	(10) Behaviour if abruptly disturbed	(11) Appearance in natural surroundings
	Epid.	Subepid.			
Aplysia punctata	Ab.	Ab.	Pedal sole and parts of mantle	Epipodial flaps brought together, pedal sole contracted	Inconspicuous in colour and attitude
Scaphander lignarius	O	Ab.	None	General contraction	Half-buried in sand
Philine quadripartita	O	Ab.	,,	,, ,,	Buried beneath sand
Berthella plumula	Ab.	O	,,	,, ,,	Not strikingly coloured but usually easy to see
Pleurobranchus membranaceus	Ab.	O	,,	General contraction, often followed by swimming motions	When swimming: conspicuous but not strikingly coloured. When creeping: camouflaged
Hermea dendritica	O	Ab. in d.p.	Whole body excluding dorsal papillae	Body contracted, dorsal papillae held erect	Difficult to see on *Bryopsis* and other Algae
Elysia viridis	O	Ab. (Fig. 1H)	Pedal sole and dorsal epidermis	Epipodial flaps brought together, pedal sole contracted	Well camouflaged among littoral and sublittoral Algae
Duvaucelia plebeia	Ab. §	O	Rhinophores and pedal sole	Rhinophores retracted, pedal sole contracted	Well camouflaged on *Alcyonium digitatum*
Tritonia hombergi	Ab. § (Fig. 1F)	O	,, ,, ,,	,, ,, ,,	,, ,, ,,
Dendronotus frondosus	Ab.	Ab. ‖	,, ,, ,,	,, ,, ,,	Well camouflaged on hydroids
Doto coronata	Ab.	Ab. in d.p.	Whole body excluding dorsal papillae	Body contracted, dorsal papillae held erect	Difficult to see on hydroids
Hero formosa	—	—	—	,, ,, ,,	Well camouflaged on hydroids
Eubranchus tricolor	O	O	—	,, ,, ,,	Never inconspicuous
Facelina auriculata	O	O	—	,, ,, ,,	,, ,,
Archidoris pseudoargus	Ab. in d.m.	Ab. in d.m.	Ventral parts of body, rhinophores and branchiae	Branchiae and rhinophores retracted; if detached from substratum foot contracted	Well camouflaged in colour, attitude, and texture
Jorunna tomentosa	Ab. in d.m.	O	,, ,, ,,	,, ,, ,,	,, ,, ,,
Acanthodoris pilosa	Ab. in d.m. (Fig. 1B)	O	,, ,, ,,	,, ,, ,,	,, ,, ,,
Onchidoris pusilla	O	Ab. in d.m. (Fig. 1D)	,, ,, ,,	,, ,, ,,	,, ,, ,,
O. fusca	Ab. in d.m.	O	,, ,, ,,	,, ,, ,,	,, ,, ,,
O. muricata	O	Ab. in d.m.	,, ,, ,,	,, ,, ,,	,, ,, ,,
Adalaria proxima	O	,,	,, ,, ,,	,, ,, ,,	,, ,, ,,
Goniodoris nodosa	O	,,	,, ,, ,,	,, ,, ,,	,, ,, ,,
Polycera quadrilineata	O	Ab. espec. in d.p.	,, ,, ,,	Body contracted, dorsal papillae held erect	Never inconspicuous
Ancula cristata	O	,,	,, ,, ,,	,, ,, ,,	,, ,, ,,

Column (8), non-mucous skin glands may be epidermal (epid.) or subepidermal (subepid.): Ab., abundant; O, not present; d.p., dorsal papillae; d.m., dorsal mantle; espec., especially.

§ Glands of two types in these two species.

‖ Subepidermal glands occur in adults, especially in the dorsal papillae (see Thompson, 1960*b*).

In addition, predation by various carnivores on pelagic gymnosomes and thecosomes is known to be widespread (personal communication from J. E. Morton). On the other hand, in a recent detailed study of the gut contents of gadoid fish from the seas around the south of the Isle of Man, no opisthobranchs were found (personal communication from A. K. Nagabhushanam).

There are instances where certain species of opisthobranchs have been wrongly said to be widely eaten by fish. A particularly glaring example of this is provided by Cott (1940), who stated that *Scaphander lignarius* was widely preyed upon by fish, giving Garstang (1890*a*) as the source of this information. While Garstang did state that *Haminoea* and *Philine* were 'largely eaten by fishes', he clearly did not claim that *Scaphander* also was. It is now necessary to inquire more deeply into Garstang's claim regarding *Haminoea* and *Philine*. He gives as his source for this Verrill (1873), but perusal of Verrill's paper shows that no mention occurs of *Haminoea hydatis* or of *Philine*. The only hard fact that emerges is that there appears to be no evidence that *Scaphander lignarius*, *Haminoea hydatis* or *Philine quadripartita* are widely eaten by fish.

DISCUSSION OF RESULTS

Feeding experiments with fish

The feeding experiments carried out in this study gave uniform results which seem to show clearly that all the opisthobranchs tested were distasteful to the fish used. It is well known that the results of such aquarium experiments must be interpreted with caution and the possibility that the fish employed might be behaving abnormally was always borne in mind. However, the obvious health of the fish, their vigorous appetites and, above all, their eagerness to take and swallow *dead* or *damaged* opisthobranchs, showed beyond reasonable doubt that some deterrent attribute possessed by healthy opisthobranchs rendered them distasteful to fish. This is not to suggest that these experiments show that fish *never* eat these opisthobranchs in nature.

Predators other than fish

Mention may be made here of some experiments with shore-crabs (*Carcinus maenas*) and with the anemones *Tealia felina* and *Anemonia sulcata*. While the anemones would often ingest opisthobranchs placed within reach of their tentacles, consistent results were impossible to obtain and their interpretation is difficult. It has already been recorded (Thompson, 1960*a*) that *Berthella* and *Pleurobranchus* were usually refused by *Tealia*; it has now been found that the eolidaceans *Facelina* and *Eubranchus* also enjoy some kind of immunity from this anemone and others. McMillan (1941) records similar results. All the other opisthobranchs tested were, however, seen to be ingested by anemones on various occasions, but never *predictably*. The significance of these results hinges on whether this predation occurs in nature; unfortunately, I can offer only the negative information that I have never seen it happen.

Tests with shore-crabs were also unsatisfactory, but more uniform; the crabs always ignored the test organisms.

Defensive attributes

Nematocysts

That eolidacean nudibranchs possess cnidosacs at the tips of their dorsal papillae has been known for many years. There can be little doubt that these nematocysts discourage fish from ingesting these molluscs, for Cott (1940) mentions that cnidarian tissues are highly distasteful to a variety of fish; my experiments confirm this. That some have been known to be devoured by fish (Homans & Needler, 1944) is not a convincing argument against the theory that one of the functions of the eolidacean cnidosacs is to deter predatory fish.

Acid secretions

Three species of opisthobranch (and two of prosobranch) gastropods are known to possess the ability to secrete a strong acid through the skin if they are roughly disturbed (Thompson, 1960 *a*). Because Bateson (1890) found fish to refuse any food which had been soaked in dilute acids it is believed that these acid-secreting gastropods are generally refused as food by fish in nature. This is supported by aquarium and other observations.

Other secretions (see Fig. 1)

In all the other opisthobranchs which have been studied in this investigation (see Table 1), skin glands have been found whose position and function can only be explained satisfactorily as defensive. They are always present in addition to the usual mucous glands associated with ciliated epithelia. They are always present in greatest abundance in the areas of the skin which would be first encountered by an inquisitive fish in nature. In species which possess dorsal papillae projecting some way out from the body, these glands are always concentrated in the papillae. Papillae of this kind are usually non-retractile, and may be rapidly regenerated if damaged. On the other hand, those dorsal processes which do not contain these glands (such as the rhinophoreal tentacles or the anal branchiae of some nudibranchs) are always retractile and are quickly concealed if the animal is disturbed. The behaviour of the opisthobranch if molested roughly is always such as to bring about the concealment of those regions of the body which are not endowed with these glands.

Histologically these defensive glands exhibit considerable diversity; they may be epidermal or subepidermal, unicellular or multicellular; their secretion may consist of fluids alone or may contain hyaline concretions; the secretion

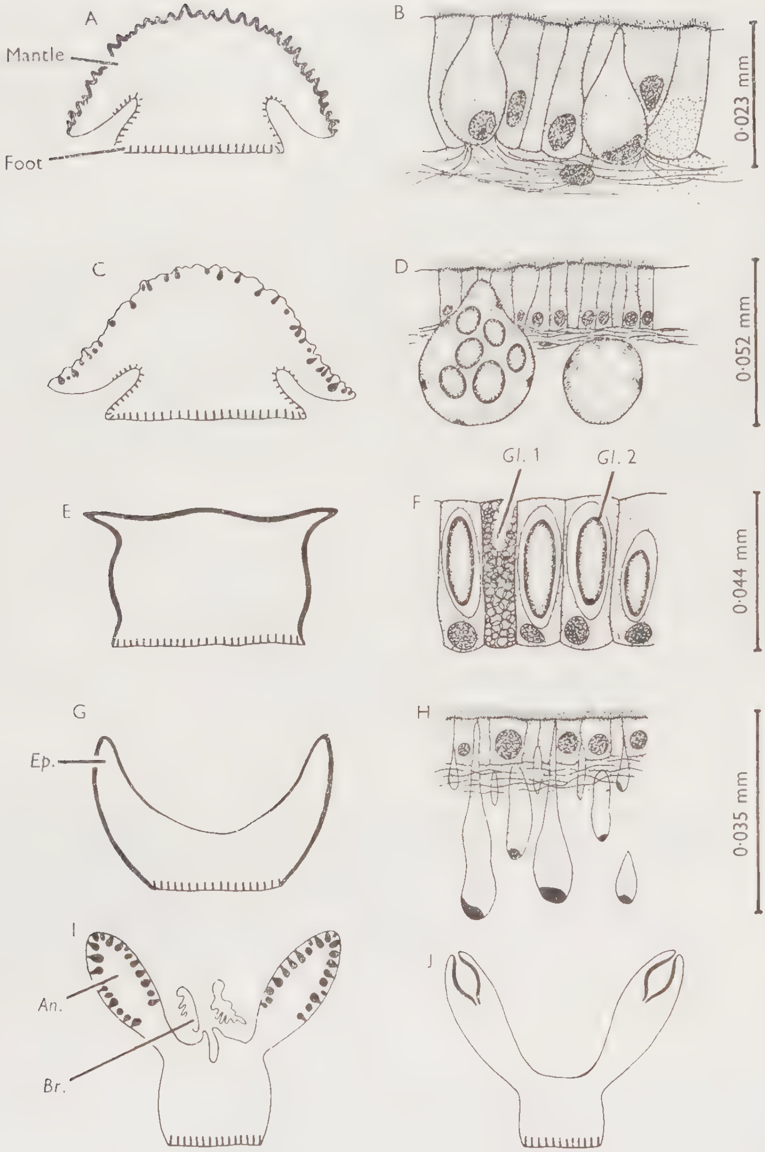

Fig. 1. Illustrating the structure and distribution of defensive glands in some representative opisthobranchs. In the diagrammatic transverse sections areas provided with defensive attributes are shown black while areas rich only in mucous glands are hatched. A, diagrammatic transverse section through *Acanthodoris pilosa*; B, portion of the dorsal integument of *A. pilosa* at greater magnification; C, diagrammatic transverse section through *Onchidoris pusilla*; D, portion of the dorsal integument of *O. pusilla* at greater magnification; E, diagrammatic transverse section through *Tritonia hombergi*; F, portion of the dorsal integument of *T. hombergi* at greater magnification; G, diagrammatic transverse section through *Elysia viridis*; H, portion of the epithelium of the epipodial flaps of *E. viridis* at greater magnification; I, diagrammatic transverse section through *Polycera quadrilineata*, passing through the level of the anus; J, diagrammatic transverse section through *Facelina auriculata*, passing through a pair of cerata and showing the position of the cnidosacs. *An.*, anal tubercle; *Br.*, anal branchia; *Ep.*, epipodial flap; *Gl.* 1, gland of type 1; *Gl.* 2, gland of type 2.

may or may not taste bitter to the human tongue. More than one type of gland may be present in a single species.

The mucus which is secreted profusely if an opisthobranch is roughly handled may decrease the animal's attractiveness as food; this mucus may even aid the effectiveness of the defensive secretions by hindering their too-rapid dispersal.

Spicules

All the dorid nudibranchs have abundant small papillae and calcareous spicules in the skin and it is probable that the spiculose texture of the mantle, while perhaps not of positive deterrent value, would diminish their attractiveness as food to a fish. It is interesting to note that sponges may be refused as food by fish in experiments (Garstang, 1890*b*).

Behaviour

The opisthobranchs studied may be classed as follows, on the basis of their behaviour both in undisturbed conditions and when abruptly disturbed:

(i) Opisthobranchs which, for most of their lives at least, behave in a way which indicates an apparent desire for concealment; this concealment may be achieved by means of coloration, attitude, texture, habitat selection, or a combination of any or all of these.

(*a*) Forms which, if abruptly disturbed, respond merely by a general contraction of the body, e.g. *Scaphander*, *Berthella*, *Philine*, *Pleurobranchus* (which may subsequently attempt to swim away). In all these forms the defensive glands are distributed over the whole naked surface of the body.

(*b*) Forms which, if abruptly disturbed, retract or otherwise conceal parts of the body which are not liberally endowed with skin glands, thus presenting a would-be predator only with those parts which are provided with defensive attributes, e.g. *Dendronotus*, *Doto*, *Aplysia*, *Elysia*, *Hermaea*, dorid and tritoniid nudibranchs.

(ii) Opisthobranchs whose behaviour is always characterized by an apparent disregard for concealment. They invariably possess well-developed dorsal papillae and, if an individual is abruptly disturbed, these papillae are held erect while the rest of the body, which is always provided to a lesser extent with any defensive attributes, is contracted, e.g. *Ancula*, *Polycera*, *Eubranchus*, *Facelina*.

Coloration

Opisthobranchs which would, on the grounds of their behaviour, fall into class (i) above are always difficult to detect (at least to the human eye) in their natural surroundings. This resemblance or camouflaging is usually achieved by a combination of the coloration of the body and of such dorsal processes as may be present, the slow-moving habits, the texture of the body and the selection of a suitable habitat (many nudibranchs are found in narrow crevices, under stones, etc., while *Scaphander* and *Philine* lie partly or wholly covered by sand).

Those opisthobranchs which fall into class (ii) above were always brightly coloured, the pigmented areas often being confined to the dorsal papillae. Since I have no evidence that any of the fish employed in my tests 'learned' to avoid any species of opisthobranch, it is best that the terms 'warning' or 'aposematic' coloration be avoided here; nonetheless there is no doubt that the colours, behaviour and form of *Ancula*, *Polycera* and the eolids investigated render these animals readily visible to the human eye both in aquaria and in the field. The inference is that they are similarly obvious to fish.

An important point which emerges from a consideration of opisthobranchs in their natural surroundings is that the usual dividing line between brightly coloured, distasteful forms on the one hand, and cryptically marked, readily edible forms on the other, does not hold. In my experiments, no facts emerged which might support a theory that the conspicuous forms (such as *Polycera* or *Eubranchus*) were any more or any less acceptable to fish than the cryptically coloured species (such as *Aplysia* or *Archidoris*). All the opisthobranchs studied were distasteful to fish. The phenomenon is not new; Cott (1940) mentions that there are a number of species of poisonous snakes which are cryptically coloured. Cott dismisses the idea that this apparent anomaly points to some deep-rooted weakness in the theory of adaptive coloration in animals in the following words (with which I am in complete agreement): '...there is nothing irreconcilable in the fact that some well-defended forms rely upon concealment as a first line of defence...while others gain an advantage by being recognized through their conspicuousness as easily as possible' (Cott, 1940, p. 155). On the other hand, it is now necessary to disagree with Cott when he states (1954, pp. 55–6): '...a broad correlation has been established between cryptic coloration and relative palatability on the one hand, and between conspicuousness and deterrent attributes on the other. Such a relationship, supported by a great body of experimental and observational evidence...is found among many groups of animals, including tectibranch molluscs (Garstang, 1889–90).'

Anomalous opisthobranchs

The species investigated in the present work were selected solely on the grounds of availability; the conclusions arrived at are thus based on a number of opisthobranchs chosen more or less at random from the British fauna. Unfortunately, several species of nudibranchs, which appear to provide exceptions to my conclusions, were not available for study. The orange-red dorid *Archidoris pseudoargus flammea* and the supposedly cryptically coloured eolid *Aeolidia papillosa* are cases in point; going farther afield, the brilliantly marked chromodorid nudibranchs of warmer seas would clearly repay further study.

This work was done while I was the holder of a Leverhulme Fellowship in the University of Liverpool. I am indebted to Mr J. S. Colman for critical reading of the manuscript and for the provision of laboratory facilities. In addition, it is a pleasure to record my indebtedness to Mr D. Eggleston, Mr R. G. Hartnoll, Mr P. J. Miller and Mr K. Reddiah, for their help in collecting the material on which this paper is based. Mr D. Eggleston also kindly gave assistance in the gustatory tests. Dr A. K. Nagabhushanam gave guidance in the literature concerning the gut contents of fish.

SUMMARY

Feeding-acceptability tests with a variety of opisthobranchiate gastropods and marine aquarium fish gave rather uniform results; in such experiments, opisthobranchs were almost invariably refused as food by fish.

Descriptions are given of the glands which, placed often in the most vulnerable yet least vital regions of the body of the opisthobranch, are believed to produce deterrent secretions.

The results of these investigations are related to facts concerning the natural history of the animals concerned, and the conclusions reached are considered in the light of modern theories concerning the adaptive coloration of animals.

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ON THE BIOLOGY OF *CALANUS FINMARCHICUS*

XI. OBSERVATIONS ON VERTICAL MIGRATION ESPECIALLY IN FEMALE *CALANUS*

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(Text-figs. 1–5)

A number of different factors have been shown to affect the vertical migration of the zooplankton, among them changes in light intensity, temperature, salinity and the presence of food (see Russell, 1927; Hardy & Paton, 1947; Cushing, 1951; Bainbridge, 1953; Harris, 1953; Moore, 1958; Banse, 1959). The object of the present study was to find out whether in female *Calanus* there was any relation between vertical migration and the degree of ripeness.

When *Calanus* were taken by tow-nettings near the laboratory it was noticed that the percentage of adult females in the ripe condition was generally greater in hauls made close to the surface than in those from deep water. For example in the spring of 1953 a series of hauls was made near the surface in Fairlie Channel where the maximum depth is about 40 m, and at 60–80 m off Garroch Head a few miles away where the depth is 115 m. Throughout the period of examination there was a much higher percentage of ripe females in the shallow than in the deep hauls (Table 1, Fig. 1). The deep hauls show the progressive ripening of the females during the spring reaching a peak in percentage ripe which coincides with the spring diatom increase in the middle of March. It also coincides with the maximum number of eggs produced by laying females. In shallow water the sequence is not so obvious because of the high percentage of ripe females at the surface most of the time.

A tendency for ripe female *Calanus* to keep in the surface waters might be expected since the eggs, which are denser than sea water (Salzen, 1956), are usually found in the upper 30 m (Nicholls, 1933). In the Clyde area adults which moult from the overwintering stock of Stage V in January and February show a marked migration, and if migration to the surface for egg-laying takes place one might expect to find a difference in behaviour of females in different stages of ripeness during the spring. It is only during early spring that a good proportion of immature and medium, as well as ripe, females is certain to be found and this is therefore the best time to study their migrations.

Vertical distribution stations were worked in the spring of three years, 1953 (2 February), 1954 (16 March) and 1959 (9 February) and on each occasion hauls were taken every 3 h for 27 h. On all three occasions the weather was calm with only light airs. There was sunshine during the day, but in 1959 the sun shone only through a haze. There was bright moonlight in 1953 and 1954 but in 1959 the night was overcast and raining. Times of sunrise and sunset are shown in the figures.

The position chosen for the observations was the deep water between the south-east of the island of Bute and the Little Cumbrae. Because of the small numbers of *Calanus* present at the end of the winter, vertical hauls with a closing net would not have given sufficient numbers for studies of ripeness. Thirty-minute hauls with 50 cm diameter coarse tow-nets (26 meshes to the inch) were therefore taken simultaneously at four depths from a trawl warp to the end of which was attached a depressor (Barnes, 1951). Tows were made at a constant speed and the depth of the nets during tows checked by an Admiralty pattern depth recorder. The top net fished just below the surface, the next at 20–25 m, the third at about 45 m and the lowest net at

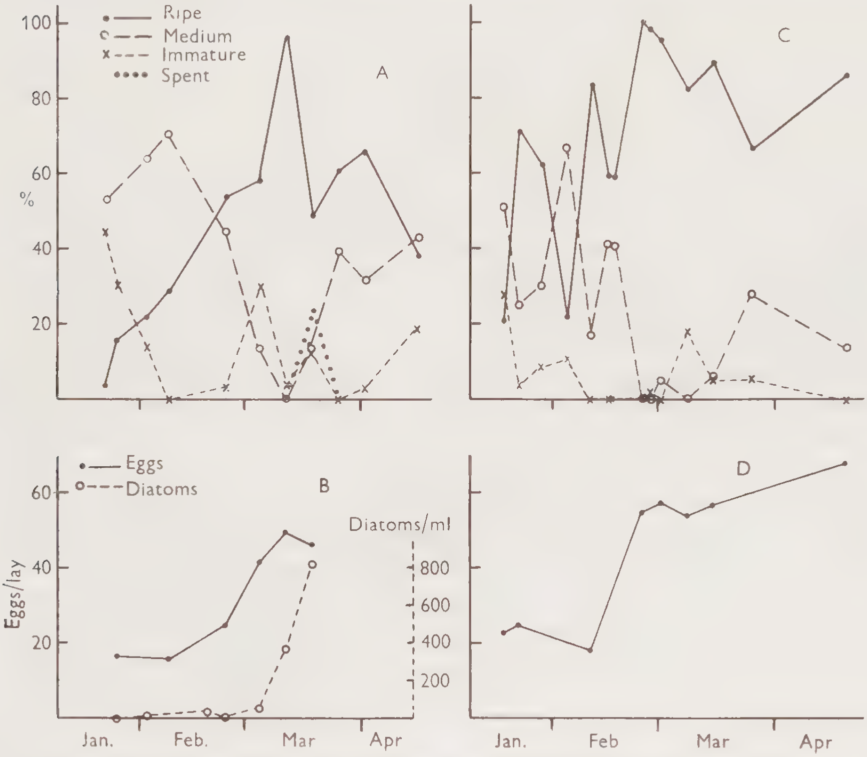

Fig. 1. Maturity of female *Calanus* in deep and shallow hauls in 1953. A and B, deep water, Garroch Head; C and D, near surface, Fairlie Channel.

60–70 m. Because of the time required for hauling and untying, the deep nets were towed for a few minutes longer than the shallow on each run. There is no simple correction which can be applied for this, but the differences are unlikely to have interfered seriously with the results.

An objection to the use of horizontal tows at a small number of depths is that important differences in the concentration of organisms might be missed. If so one would expect to find changes in the total numbers from top to bottom during the 27 h. There was in fact a rise in total numbers in the early evening in two of the years which may have been because of an influx from below the depth of the bottom net. Otherwise total numbers remained reasonably constant. The percentage of the total catch in different stages and states of maturity also remained fairly constant throughout.

TABLE 1. MATURITY IN SPRING, 1953

		% Females						
Date	No. examined	Immature	Medium	Semi-ripe	Ripe	Spent	Eggs per lay	Diatoms (cells/ml.)
				Garroch Head, 60–80 m.				
2 Jan.	47	45	43	9	4	0	—	—
26 Jan.	51	31	28	26	16	0	17	0
2 Feb.	536	14	20	44	22	0	—	10
9 Feb.	51	0	22	49	29	0	16	—
19 Feb.	—	—	—	—	—	—	—	35
24 Feb.	39	3	3	41	54	0	25	0
5 Mar.	40	30	10	3	58	0	42	50
12 Mar.	25	4	0	0	96	0	50	370
19 Mar.	45	13	4	9	49	24	46	818
26 Mar.	31	0	7	32	61	0	—	—
2 Apr.	32	3	13	19	66	0	—	—
16 Apr.	32	19	34	9	38	0	—	—
				Fairlie Channel, near surface				
19 Jan.	43	28	23	28	21	0	23	
23 Jan.	56	4	9	16	71	0	25	
29 Jan.	71	9	17	13	62	0	—	
5 Feb.	45	11	38	29	22	0	—	
11 Feb.	23	0	4	13	83	0	18	
16 Feb.	87	0	2	39	59	0	—	
17 Feb.	27	0	0	41	59	0	—	
25 Feb.	20	0	0	0	100	0	55	
27 Feb.	50	2	0	0	98	0	—	
2 Mar.	21	0	0	5	95	0	58	
9 Mar.	28	18	0	0	82	0	54	
16 Mar.	18	6	6	0	89	0	57	
26 Mar.	35	6	14	14	66	0	—	
20 Apr.	14	0	7	7	86	0	68	

The tow-nettings were fixed in 5% formalin and afterwards the numbers of males, females and Stage V counted in aliquot samples from each haul. When numbers allowed it at least 200 of the females were taken for staining and clearing to determine ripeness.

Three different methods of staining were tried. In the first year (1953) the females were stained in methylene blue, dehydrated in dioxan and cleared and examined in creosote. This sometimes gave a very clear picture but the results were not consistent because the largest and ripest eggs hardly stained at all and were easy to miss. Eventually samples of this series were stained with celestine blue B (see below).

In 1954 the stain used was borax carmine and the examination was made in xylol. This method proved fairly satisfactory and the results were later checked against the celestine blue method. Staining with celestine blue B (Gray, 1958) proved the best method and was adopted for the 1959 hauls. We should like to thank Dr H. F. Steedman of the Zoology Department of the University of Glasgow for suggesting the method and for his help.

The specimens were put in a glass tube closed at the lower end by coarse bolting silk, and were washed and then stained in celestine blue B (14 ml. to 86 ml. 1% acetic acid). They were then taken through a series of alcohols and cleared in diethyl phthalate.

Unfortunately the living females especially when ripe look rather different from the fixed, stained and cleared specimens and the categories chosen, immature, medium and ripe, do not necessarily correspond exactly to those used for living material (Marshall & Orr, 1952). The eggs appear smaller and the ripe female less full of eggs. In February and March, however, the number of large eggs in a ripe female is very much smaller than it is later in the year.

The ripest eggs do not as a rule stain so heavily as the unripe, and the arbitrary criterion we have used in distinguishing the ripe from the medium is that there should be a row of these larger and paler eggs in the lower part of the oviduct (Fig. 2 C). There is no such definite criterion to distinguish the immature from the medium, but in the immature the ovary is small, the oviducal diverticula are represented by two short single rows of small eggs not extending to the front of the head and the oviducts have a single row, often discontinuous, of small eggs (Fig. 2 A). In the medium, the oviducal diverticula extend almost to the front of the head and may have more than one row of eggs each; the eggs in the oviduct are larger and pressed more closely together forming a single or a double row (Fig. 2 B). As a rule, in distinguishing the different stages, most weight was given to the appearance of the oviducts.

MIGRATIONS

A study of the vertical distribution of *Calanus* in spring has already been made for a deep station in this area (Nicholls, 1933). The four distributions, all of the same generation, within 8 weeks (although in different years), and within the same area, might be expected to resemble one another closely, but in fact they do not.

The earliest, that of Nicholls on 25 January 1932, although based on rather small numbers, shows the clearest results. Apart from this it differs from the rest in having been done in much deeper water and with a closing net. It shows the usual pattern for the overwintering generation in which the females migrate most, in close agreement with light changes, the males migrate less, and the Stage V hardly at all.

In 1959 (9–10 February) the behaviour of females and males followed this pattern (Fig. 3 and Table 2), but the Stage V also showed a distinct migration slightly more marked than that of the males. From 9.00 to 15.00 h all stages were concentrated in the bottom net (62 m), but between sunset and sunrise the distribution was much more even throughout the water column with a tendency for the females to be concentrated in the upper two nets and the males and Stage V in the lower two.

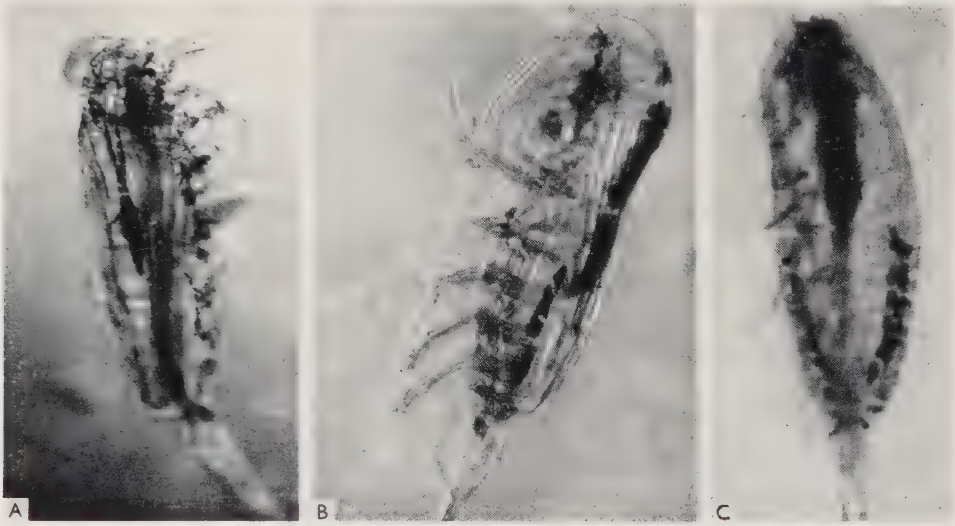

Fig. 2. Female *Calanus* stained with celestine blue. A, immature: the ovary, oviducal diverticula and right oviduct are visible. B, medium: oviducal diverticula extend farther forward and eggs are larger. C, ripe: note the two sizes of eggs in the oviduct.

In 1953 (2–3 February) the main difference was that the *Calanus* were higher in the water (Fig. 3), the highest numbers being usually in the net at 45 m in spite of clearer sunshine than in 1959. Apart from this the females showed the usual migration upwards between sunset and sunrise. This movement was less marked in the males and Stage V. All, however, behaved less regularly than in 1933 or in 1959.

In 1954 (17–18 March) the behaviour was surprisingly different. A considerable proportion of all the *Calanus* remained in the two top nets throughout the 27 h and at 9.00 and 12.00 h, the brightest hours, were even more concentrated there, a distribution quite opposite to those found earlier in

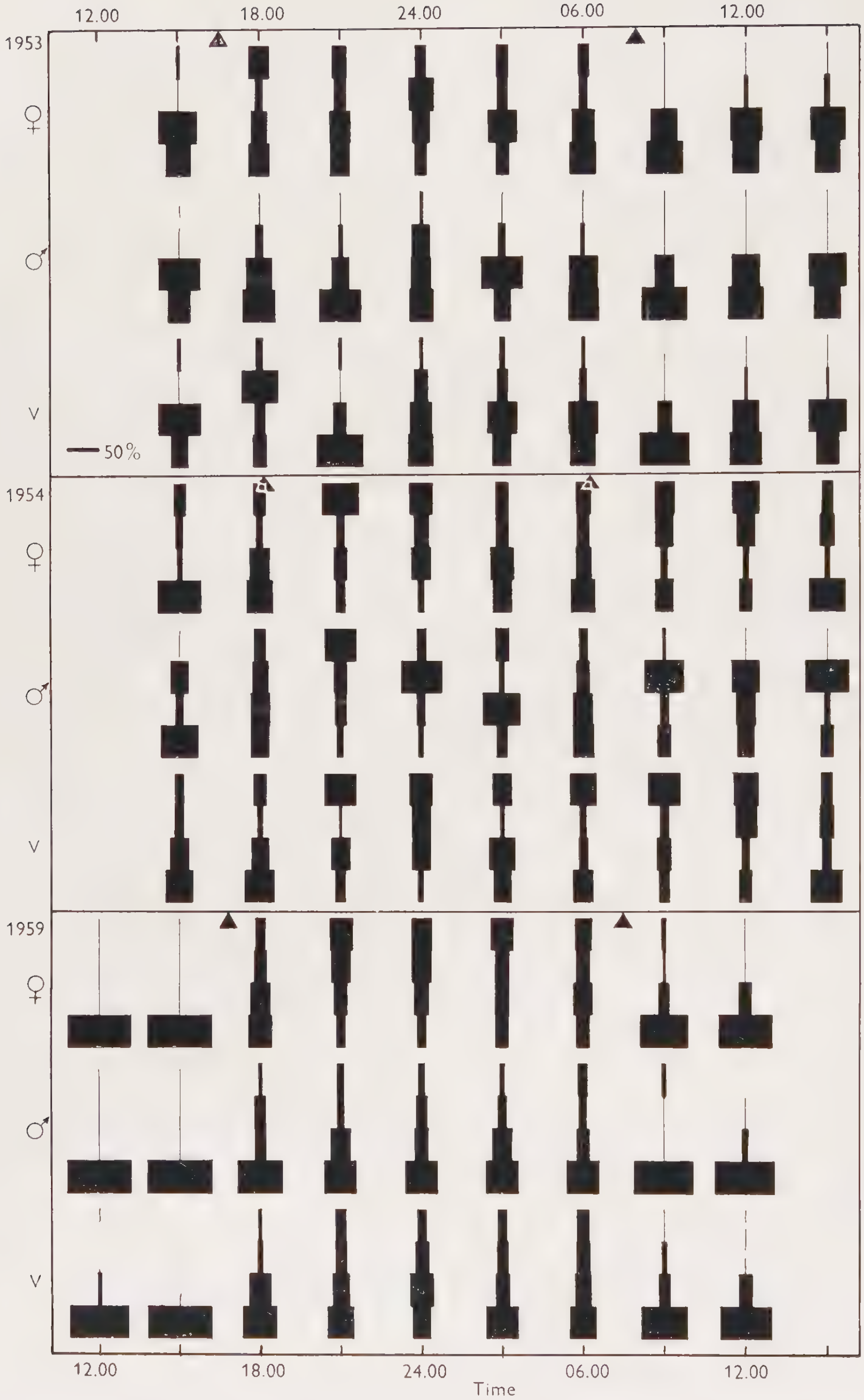

Fig. 3. Vertical distribution of male, female, and Stage V *Calanus* at four depths. The arrows show times of sunset and sunrise.

TABLE 2. VERTICAL DISTRIBUTION OF FEMALE, MALE AND STAGE V *CALANUS*

		2–3 February 1953							16–17 March 1954							9–10 February 1959					
		♀		♂		V			♀		♂		V			♀		♂		V	
Haul	Time	No.	%	No.	%	No.	%		No.	%	No.	%	No.	%		No.	%	No.	%	No.	%
I. 1	15.00	77	1·3	9	0·4	5	1·3	15.00	1013	23·9	2	1·4	61	13·4	12.00	13	0·3	2	0·6	0	0
2		355	5·9	38	1·6	27	7·0		603	14·2	42	28·4	65	14·3		32	0·8	1	0·3	5	2·3
3		3380	56·7	1480	64·4	250	65·4		359	8·5	19	12·8	133	29·3		119	2·9	3	1·0	14	6·4
4		2150	36·1	770	33·5	100	26·2		2260	53·4	85	57·4	195	42·9		3928	96·0	302	98·1	200	91·3
II. 1	18.00	3750	32·5	80	2·2	110	10·4	18.00	547	17·9	16	18·2	46	19·2	15.00	10	0·1	6	1·0	1	0·2
2		1400	12·1	440	12·0	600	56·5		344	11·3	21	23·9	18	7·5		55	0·6	2	0·3	4	0·6
3		2670	23·1	1410	38·4	160	15·1		983	32·2	26	29·6	66	27·5		21	0·2	1	0·2	5	0·8
4		3730	32·3	1740	47·4	190	17·9		1175	38·5	25	28·4	110	45·8		8990	99·1	580	98·5	650	98·5
III. 1	21.00	1690	20·7	80	2·8	20	4·0	21.00	2410	45·8	95	48·5	250	48·3	18.00	995	15·8	11	5·0	18	6·7
2		1600	19·6	170	6·0	10	2·0		795	15·1	40	20·4	24	4·6		1150	18·2	18	8·3	23	8·5
3		2590	31·7	780	27·4	110	22·0		1126	21·4	37	18·9	159	30·7		2024	32·1	35	16·0	89	33·1
4		2280	27·9	1810	63·7	360	72·0		936	17·8	24	12·2	85	16·4		2134	33·9	154	70·6	139	51·6
IV. 1	24.00	602	16·6	40	3·3	14	5·7	24.00	1395	20·9	20	13·5	155	35·4	21.00	2357	36·8	61	12·6	67	18·3
2		1385	38·1	345	28·9	55	22·5		2045	30·7	95	64·2	125	28·5		1882	29·6	57	11·8	60	16·3
3		975	26·8	370	31·0	85	34·8		2220	33·3	20	13·5	120	27·4		1281	20·1	138	28·5	95	25·9
4		670	18·4	440	36·8	90	36·9		1010	15·1	13	8·8	38	8·7		863	13·5	228	47·1	145	39·5
V. 1	03.00	531	17·7	26	2·3	14	8·1	03.00	925	13·1	30	20·3	75	28·0	24.00	1808	31·8	54	10·9	66	13·7
2		468	15·6	105	9·2	29	16·8		1315	18·7	8	5·4	18	6·7		1731	30·5	83	16·7	107	22·3
3		1390	46·4	725	63·4	80	46·2		2795	39·7	85	57·4	105	39·2		1274	22·4	109	21·9	170	35·4
4		607	20·3	287	25·1	50	28·9		2005	28·5	25	16·9	70	26·3		869	15·3	252	50·6	137	28·5
VI. 1	06.00	673	16·4	40	2·2	13	5·3	06.00	931	22·7	18	13·3	83	40·1	03.00	2049	35·9	29	5·7	65	13·3
2		467	11·4	110	6·0	23	9·4		951	23·2	30	22·2	26	12·6		1304	22·9	68	13·3	80	16·4
3		1430	34·7	850	46·2	110	44·7		997	24·3	42	31·1	30	14·5		1086	19·2	152	29·9	108	22·2
4		1545	37·5	840	45·7	100	40·6		1219	29·8	45	33·3	68	32·9		1264	22·1	260	51·0	234	48·0
VII. 1	09.00	46	1·1	13	0·7	3	1·1	09.00	1983	25·5	7	4·1	171	47·4	06.00	1491	26·9	44	15·3	59	17·3
2		83	2·0	15	0·8	6	2·1		3167	40·7	107	62·9	52	14·4		1196	21·6	32	11·1	66	19·3
3		1690	40·3	560	30·1	60	21·5		940	12·1	24	14·1	77	21·3		1651	29·7	62	21·6	84	24·6
4		2370	56·5	1270	68·3	210	75·3		1694	21·8	32	18·8	61	16·9		1210	21·8	149	51·9	133	38·9
VIII. 1	12.00	132	2·2	8	0·5	7	2·3	12.00	1930	40·8	2	2·0	86	35·3	09.00	247	5·4	15	5·1	9	3·3
2		477	7·9	60	3·6	20	6·5		1703	36·0	45	44·0	82	33·6		224	4·9	5	1·7	18	6·5
3		3040	50·5	680	41·3	130	42·3		351	7·4	28	27·4	32	13·1		750	16·4	7	2·4	50	18·0
4		2370	39·3	900	54·6	150	48·8		745	15·8	27	26·5	44	18·0		3356	73·3	268	90·8	200	72·2
IX. 1	15.00	150	2·6	26	2·2	4	1·9	15.00	660	15·3	5	3·9	37	16·8	12.00	13	0·3	0	0·0	3	1·0
2		359	6·3	34	2·9	13	6·3		1348	31·2	86	66·2	47	21·4		33	0·8	4	1·0	2	0·7
3		2960	52·1	650	55·1	120	58·0		422	9·8	12	9·2	31	14·1		697	17·6	29	7·2	63	20·5
4		2210	38·9	470	39·8	70	33·8		1893	43·8	27	20·8	105	47·7		3220	81·3	368	91·7	240	77·9

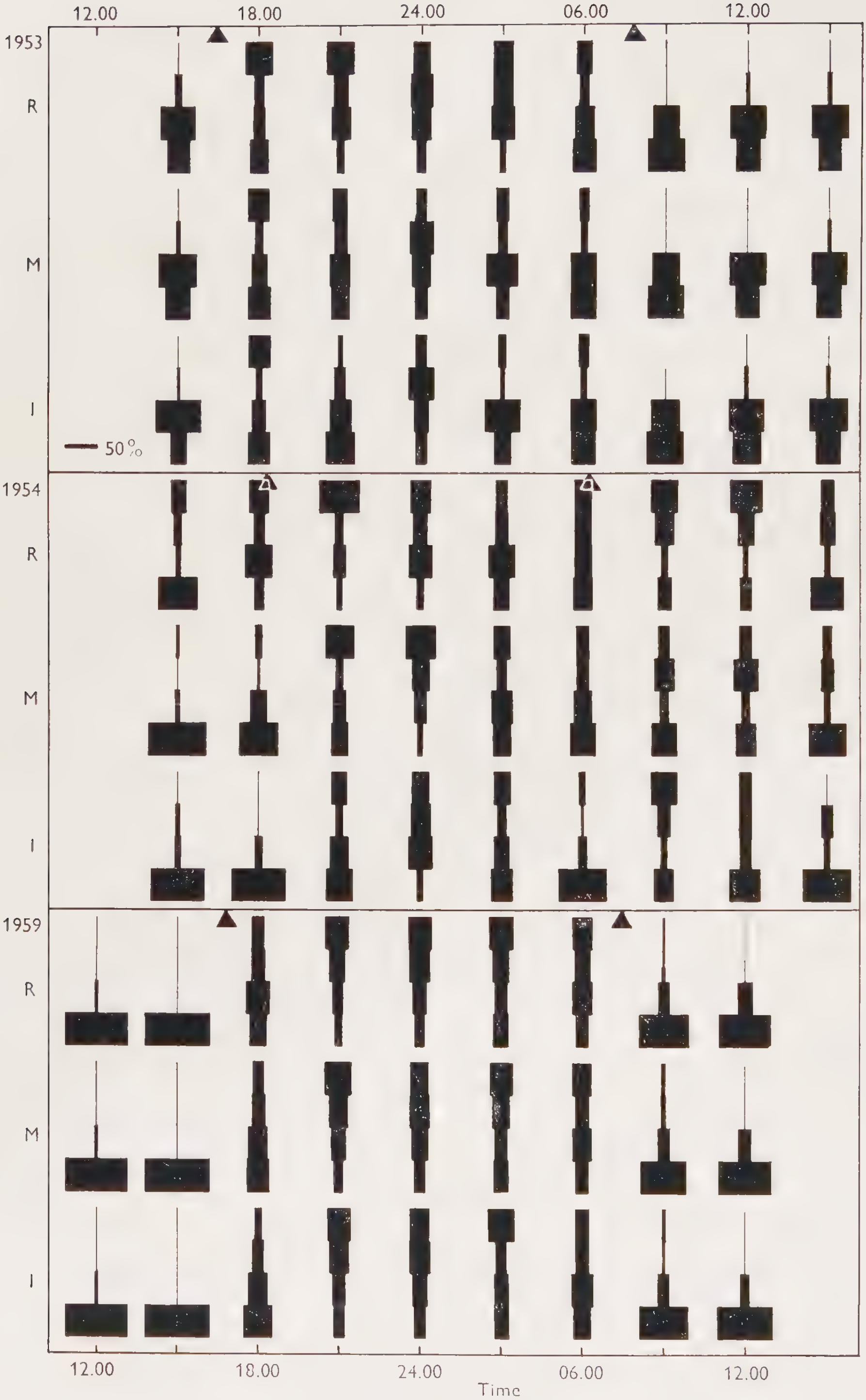

Fig. 4. Vertical distribution of ripe (R), medium (M), and immature (I) female *Calanus* at four depths.

the year. There was, however, a rise from the bottom from 18.00 to 24.00 h followed by a descent till 6.00 h and then the curious secondary rise at 9.00 and 12.00 h. At 15.00 h the distribution on the first day differed considerably from that on the second. The weather was hazy instead of clear sunshine. More of all stages were higher in the water on the second day and the males were actually richest in the second net.

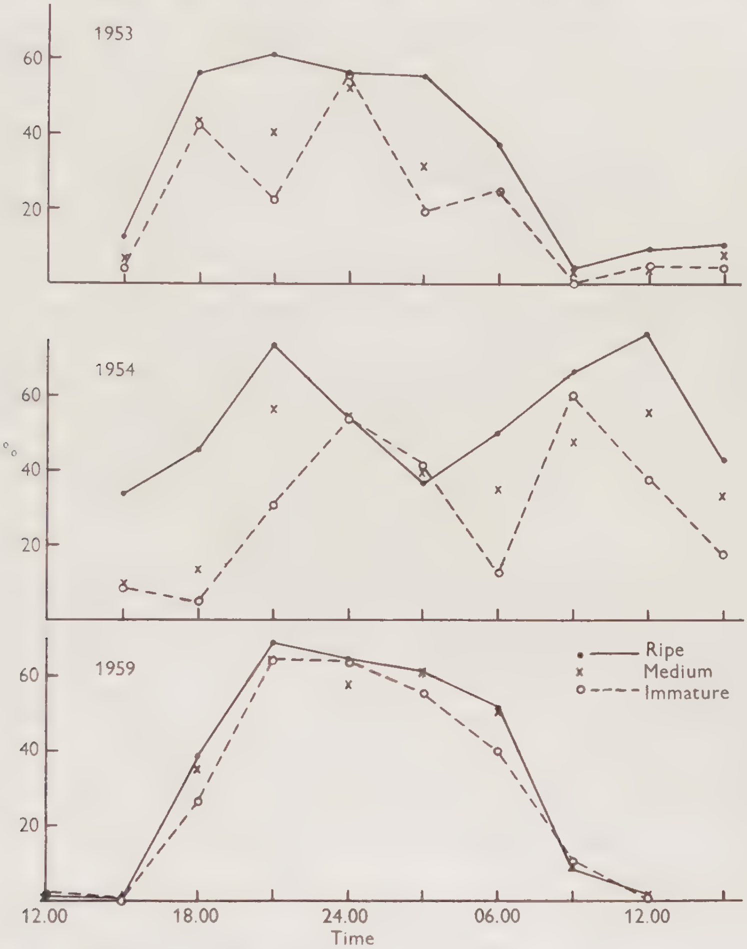

Fig. 5. Percentage of ripe and immature female *Calanus* in the two top nets.

Figs. 4 and 5 and Table 3 show the vertical distribution of the females when separated into three states of maturity—ripe, medium and immature. In 1953 and 1959 all resemble one another closely, but the immature show a slightly later and less marked rise and an earlier descent than the ripe. This is perhaps more clearly seen in Fig. 5, where the percentage of ripe and

TABLE 3. VERTICAL DISTRIBUTION OF RIPE, MEDIUM AND IMMATURE ♀ *CALANUS*

		2–3 February 1953							16–17 March 1954								9–10 February 1959						
		Ripe		Medium		Immature			Ripe		Medium		Immature			Ripe		Medium		Immature	
Haul	Time	No.	%	No.	%	No.	%	Time	No.	%	No.	%	No.	%	Time	No.	%	No.	%	No.	%
I. 1	15.00	9	0·9	23	0·9	6	0·4	15.00	522	21·9	31	6·6	4	1·1	12.00	5	0·3	5	0·4	3	0·3
2		114	11·7	160	6·0	59	3·6		282	11·9	10	2·1	28	7·6		9	0·5	12	0·9	12	1·4
3		524	53·9	1476	55·1	1143	69·9		166	7·0	17	3·6	30	8·1		57	3·0	40	3·0	25	2·9
4		322	33·1	1018	38·0	426	26·0		1408	59·2	411	87·6	308	83·2		1837	96·3	1277	95·7	823	95·3
II. 1	18.00	818	40·1	1459	32·1	1330	33·6	18.00	435	30·1	47	9·7	16	2·7	15.00	5	0·2	3	0·1	3	0·1
2		331	16·2	506	11·1	356	9·0		221	15·3	17	3·5	17	2·9		19	0·7	22	0·6	16	0·7
3		339	16·6	1108	24·4	905	22·9		600	41·5	122	25·1	66	11·2		7	0·2	7	0·2	7	0·3
4		552	27·1	1477	32·5	1363	34·5		189	13·1	300	61·7	489	83·2		2884	98·9	3734	99·2	2364	98·9
III. 1	21.00	145	6·9	773	21·6	628	39·4	21.00	1754	61·4	219	44·1	73	23·3	18.00	423	17·5	370	16·7	185	11·2
2		321	15·4	677	18·9	355	22·3		350	12·3	61	12·3	24	7·7		506	20·9	407	18·3	253	15·3
3		691	33·0	1144	31·9	432	27·1		531	18·6	90	18·1	86	27·4		862	35·6	680	30·6	498	30·2
4		932	44·6	989	27·6	179	11·2		221	7·7	127	25·6	131	41·7		627	25·9	765	34·4	715	43·3
IV. 1	24.00	181	23·9	254	16·3	159	15·7	24.00	805	32·0	400	45·6	45	25·0	21.00	945	39·5	782	38·7	653	33·4
2		250	33·1	568	36·5	412	40·8		565	22·5	234	26·6	53	29·4		702	29·4	524	25·9	603	30·9
3		218	28·8	433	27·8	248	24·6		883	35·2	166	18·9	66	36·7		482	20·1	442	21·9	370	18·9
4		107	14·2	301	19·3	191	18·9		259	10·3	78	8·9	16	8·9		262	11·0	272	13·5	329	16·8
V. 1	03.00	196	28·8	228	17·8	95	12·4	03.00	396	17·6	235	25·2	64	26·9	24.00	716	33·0	528	28·7	562	32·7
2		184	27·0	173	13·5	53	6·9		430	19·1	136	14·6	34	14·3		683	31·5	528	28·7	528	30·7
3		239	35·1	615	47·9	418	54·5		882	39·2	305	32·7	57	23·9		461	21·2	475	25·8	367	21·3
4		62	9·1	267	20·8	201	26·2		541	24·0	256	27·5	83	34·9		310	14·3	310	16·8	261	15·2
VI. 1	06.00	195	22·7	273	14·0	161	15·0	06.00	359	25·4	133	19·2	27	8·6	03.00	791	35·6	693	33·1	576	40·3
2		125	14·5	205	10·5	114	10·6		348	24·6	110	15·9	13	4·2		572	25·8	559	26·7	214	15·0
3		250	29·1	735	37·6	403	37·5		343	24·2	177	25·6	43	13·7		360	16·2	398	19·0	322	22·5
4		290	33·7	738	37·8	397	36·9		365	25·8	271	39·2	230	73·5		495	22·3	446	21·3	318	22·2
VII. 1	09.00	17	2·2	21	1·0	0	0·0	09.00	1126	39·4	168	16·5	100	40·7	06.00	557	28·4	625	29·0	317	22·0
2		19	2·5	44	2·2	2	0·2		784	27·4	320	31·4	48	19·5		452	23·1	483	22·4	260	18·1
3		296	38·8	867	42·4	477	44·2		298	10·4	143	14·0	25	10·2		570	29·1	607	28·1	474	33·0
4		430	56·4	1110	54·3	600	55·6		648	22·7	387	38·0	73	29·7		381	19·4	442	20·5	387	26·9
VIII. 1	12.00	45	3·0	63	2·2	10	0·8	12.00	1140	50·3	90	17·7	34	17·9	09.00	88	4·3	88	6·1	70	6·2
2		99	6·6	192	6·8	51	4·3		597	26·3	195	38·3	38	20·0		87	4·3	85	5·8	52	4·6
3		802	53·2	1565	58·6	608	51·4		152	6·7	61	12·0	29	15·2		354	17·3	256	17·6	179	16·0
4		562	37·3	994	35·3	512	43·4		379	16·7	162	31·9	89	48·6		1510	74·1	1025	70·5	820	73·2
IX. 1	15.00	62	4·1	49	1·8	7	0·7	15.00	326	19·9	109	13·2	2	1·2	12.00	5	0·4	3	0·2	5	0·4
2		98	6·5	176	6·5	38	3·8		382	23·2	166	20·2	29	16·7		13	0·9	5	0·4	15	1·2
3		836	55·5	1436	53·1	599	60·2		121	7·4	75	9·1	16	9·2		286	20·8	230	17·2	181	14·5
4		509	33·8	1044	38·6	351	35·3		811	49·4	473	57·4	127	73·0		1074	78·0	1101	82·2	1046	83·8

immature in the two top nets is shown. In general the medium state females are intermediate between ripe and immature.

In 1954 the immature were concentrated in the bottom net from 12.00 to 18.00 h and showed an irregular rise in the dark with a curious dip at 6.00 h. The ripe, on the other hand, tended to concentrate at the surface even in the daylight hours and to be more evenly distributed in the dark. As before the distribution of the medium state was intermediate.

Calanus finmarchicus is the dominant form in the Clyde sea area, but during the winter an appreciable proportion of the *helgolandicus* form may be present. However their numbers were too small for a study of their diurnal migration except in the spring of 1954. The females were then much more mature than those of the *finmarchicus* form, about 90% ripe as against 70%.

The pattern of vertical migration differed from that for the *finmarchicus* in that the tendency to concentrate in the upper nets during the day was more marked. During the night, on the other hand, they were deeper than the *finmarchicus*. When the females were separated into ripe, medium and immature, it was seen that, as with the *finmarchicus* form, the ripe tended to be higher in the water for most of the time. The immature were too scarce to give reliable results.

DISCUSSION

The state of the gonad can now be added to the other factors which influence vertical migration. It is most easily distinguished in females, and it is the female which might be expected to come to the surface at night. Apart from the necessity for feeding, eggs are at this time of year laid mainly between midnight and 2.00 h (Harding, Marshall & Orr, 1951). In the early spring months before the diatoms have begun to increase in numbers these factors may not be operative. Phytoplankton is scarce and evenly distributed and, although there are often some eggs laid in February, the majority seem to be laid in March or even April. However, the hauls taken in deep water and near the surface in 1953 (Fig. 1) show that the percentage of ripe females is higher near the surface even in February.

A surprising feature of the results is the difference in migration in different years. The most unexpected difference is the behaviour of the Stage V. During the winter they are normally found in deep water, and Nicholls (1933) found that they did not migrate. We, on the other hand, have found that in all three years they migrated almost as much as the adults. Another point of interest is that the *Calanus* were deeper in 1959 than in the two other years although their behaviour was similar in 1953 and 1959.

On many occasions in 1950 and 1951 Gauld examined catches from three different depths throughout 24 h in the Clyde sea area and he says (1953): 'that only on seven of the thirteen occasions on which hauls were taken, were the catches of the top net distinctly greater in darkness than in daylight'. This also shows how variable vertical migration may be from year to year and perhaps even from month to month.

The tendency of the *Calanus* in 1954 to remain near the surface even at noon on the second day was surprising. It almost looks as though two populations were present, a surface living and a deep living. The first generation of the year, which does live mainly at the surface, has appeared as adults in these waters as early as the middle of March and it seemed possible that there was here a mixture of the overwintering and the first generation. Had two generations been present, however, the immature should have belonged to the later surface-living rather than to the overwintering one and actually the immature were found concentrated in the bottom net from 12.00 to 18.00 h. In addition, the clearest indication of the presence of the adults of the first generation came nearly a month later, on 16 April, when the proportion of males and of unripe females rose considerably, and 30% of the latter were carrying spermatophores. An examination too of nearly 6000 measurements of the lengths of the females in the vertical distribution hauls showed that the size curve was symmetrical with no suggestion of two modes as would have been expected had the two generations been mixed.

The chief difference between the 1954 observations and those for other years is that the station was worked a month later. In 1953 and 1959 the ratio of ripe:medium:immature was about 20:50:30 while in 1954 it was 70:20:10. It is possible that the behaviour of females may show a gradual change with advancing ripeness rather than an abrupt change with the generation. The anomalous results for the females might thus be explained by the fact that the majority were ripe and were staying near the surface to lay their eggs; in this case one would have expected the Stage V and males to have behaved normally. Their distributions, however, are also anomalous although less markedly so.

Banse (1959) has stressed the importance of temperature and salinity gradients for the vertical distribution of the zooplankton. It seems improbable that here the gradients in either temperature or salinity had a measurable effect on the migrations recorded. Water samples were taken at the stations and the vertical gradient in temperature in 1959 was less than 1° C (7·1–7·8° C) and in salinity less than one part per thousand (33·15–32·57‰). In 1959, however, the water was warmer than in the other two years (1953, 6·3–7·3° C; 1954, 6·2–6·9° C).

SUMMARY

A comparison of vertical distribution stations worked in several different years shows that the diurnal vertical migration varies considerably from one to another. The state of maturity of the females influences it in that ripe females migrate more and remain higher in the water than immature.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Alexander, R. McN., 1959. The physical properties of the swimbladders of fish other than Cypriniformes. *J. exp. Biol.*, Vol. 36, pp. 347–55.

The properties of the swimbladders of seventeen species of teleost from the orders Clupeiformes, Anguilliformes, Gasterosteiformes, Gadiformes and Perciformes were examined. Determinations of sinking factor and swimbladder volume are reported. In no case could excess internal pressure be detected, and the new swimbladder wall was found to exercise no appreciable constraint on changes of buoyancy of the fish with depth. These fish are contrasted with the Cypriniformes, where excess internal pressure has been found in all species examined, and where changes of swimbladder volume and so of buoyancy with depth are reduced by the constraint of the swimbladder wall.

The marine species examined were studied at the Plymouth Laboratory. R. MCN. A.

Cooper, L. H. N., 1958. Océanographie expérimentale en Méditerranée. *Trav. Cent. Rech. Etud. océangr.*, T. 3, Fasc. 2, pp. 17–25.

The Ligurian and Balearic Seas provide a small-scale model for the study of the formation of bottom water in the North Atlantic. It is suggested that (*a*) nowhere in the deep ocean does truly vertical mixing between surface and bottom occur but that sinking occurs helically and waters may be re-cycled several times during the process; (*b*) the abyssal water of the Western Mediterranean is composite and derived firstly from water from the Eastern Mediterranean by way of the Sicily–Tunis and Capraia Channels at 300–400 m depth and secondly from water over the narrow shelf of the Cote d'Azur, Riviera di Ponente and coast of Tuscany cooled by the mistral and tramontana winds; (*c*) when the strong winds drop, the heavy water cascades over the edge of the shelf and at a depth of 300–400 m mixes with the water from the Capraia Channel to produce a very heavy water which sinks not vertically but along an inclined plane. Whilst sinking it may incorporate enveloping water, poor in oxygen, which may be recycled in the abyss. L. H. N. C.

Cooper, L. H. N., 1959. Calm patch. *Yachting World*, Vol. 3, p. 250.

An explanation is offered of a calm patch about 30 miles long and a cable in width observed by a yachtsman in a rough sea off the coast of Portugal. The phenomena may have been a convergence over the continental edge between conflicting currents. In this an oil film of biological origin had become concentrated. L. H. N. C.

Day, Alan A., 1959. The continental margin between Brittany and Ireland. *Deep-Sea Res.*, Vol. 5, pp. 249–65.

The continental slope between Brittany and Ireland is steep and cut by many canyons, with the exception of the central region which forms a broad smooth spur. Scarps up to 110 miles in length are associated with the continental margin, and these, together with the steep areas of the slope proper, are considered very probably to have been developed by faulting. Cores and bottom samples from the area are shown mainly to represent Recent and Pleistocene deposits, with the exception of three which represent Tertiary and possibly Cretaceous strata.

New names applied to topographic features in the area are: Meriadzek Terrace, Goban Spur and Pendragon Scarp.

A. A. D.

HAWES, F. B., 1958. Preliminary observations on the settlement of the actinula larva of the *Tubularia* larynx (Ellis & Solander). *Ann. Mag. nat. Hist.*, Ser. 13, Vol. 1, pp. 147–55.

This paper records the results of an uncompleted study of the actinula. The latter are discharged by movements of the gonophore at differing stages of development. Attachment to a substrate is effected initially by nematocysts at the tips of the aboral tentacles. The nematocysts are frequently not fully developed when the actinula is discharged with the result that the free-living stage is prolonged.

Movements described by previous authors as walking, swimming and substrate testing appear to be parts of an inherent rhythmic cycle seen more clearly in the adult.

F. B. H.

DAY, A. A., HILL, M. N., LAUGHTON, A. S. & SWALLOW, J. C., 1956. Seismic prospecting in the western approaches of the English Channel. *Quart. J. Geol. Soc. London*, Vol. 112, p. 15.

On the basis of the measured seismic velocities, the layering found at 25 seismic stations in the area of the western approaches of the English Channel is divided into four classes which are respectively correlated with semi-consolidated Cretaceo-Tertiary sediments, the New Red system, the palaeozoic system, and a metamorphic basement. The last of these appears to form a long deep trough. The palaeozoic floor is depressed in a trough of somewhat variable depth, bounded on the north by an outcrop of the metamorphic basement which is probably a westward extension of the upthrust Lizard-Start metamorphic belt. Contour maps of the layering are produced.

A. A. D.

KAMPA, E. M., BODEN, B. P. & ABBOTT, B. C., 1959. Electrical response to illumination of the Euphausiid Crustacean eye. *Nature, Lond.*, Vol. 183, pp. 1820–1.

The electrical potentials developed in the eyes of three species of euphausiid crustaceans, *Meganyctiphanes norvegica*, *Euphausia pacifica* and *Nematoscelis difficilis*, during stimulation by light have been measured. Silver-silver chloride gauze served as the indifferent electrode. The recording microelectrode, which penetrated the eye, was made of tungsten wire. Signals from the microelectrode were amplified and recorded with an oscilloscope or an ink-writer. Intensity, duration and colour of the stimulating light flash were varied. Response to a 100 msec flash is rapid with a small *a*-wave lasting about 20 msec, a main response which reaches a peak in about 40 msec, and a final overshoot in the other direction. Over a defined range of light intensities, the height of the main response varies directly with the logarithm of the intensity. At the upper end of this range the signal reaches a limiting value of 200–300 μV. Flashes of longer duration induce response at both on and off. The euphausiid eye is most sensitive to blue-green light.

E. M. K.

WICKSTEAD, J. H. 1959. A predatory copepod. *J. Anim. Ecol.*, Vol. 28, pp. 69–72.

During analysis of some Indo-West-Pacific plankton it was noted that the copepod *Candacia bradyi* A. Scott very frequently had another animal grasped in its 1st maxillipedes. This animal was usually a chaetognath—*Sagitta enflata* Grassi. A detailed analysis was made of some samples and, after due consideration was given to the fact that it was preserved material which was being dealt with, the evidence is that this species of copepod is wholly carnivorous. Some selectivity is shown in its feeding, the prey normally being a chaetognath, particularly *S. enflata*. It is shown that the 1st maxillipedes are not suitable for filter feeding but do have all the essentials of a raptorial organ.

The suggestion is also made that *Tortanus gracilis* (Brady) is mainly, probably wholly, carnivorous, feeding mainly on other copepods.

J. H. W.

BOOK REVIEW

SEA SHELLS OF TROPICAL WEST AMERICA. MARINE MOLLUSKS FROM LOWER CALIFORNIA TO COLOMBIA

By A. MYRA KEEN

Stanford University Press. London: Oxford University Press. £5.

This book is the first attempt to catalogue and describe as a whole the marine shells of the Panamanian province, covering the west coast of Central America between the Gulf of California and Colombia. The marine fauna of this region is perhaps remarkable in showing greater resemblances to that of the Caribbean than to the Indo-Pacific regions, due to a continuity between the two areas through a natural Panama canal or seaway during former geological periods. The scope of this work lies between that of a monograph and a collector's handbook, but descriptions are included of all species found within the 100 fathom line, save the smaller gastropods which are cited only by genus. Dichotomous keys for identification are included where necessary, each species being briefly described, and in most instances illustrated. The reader will be gratified to find that the illustrations lie invariably on the same or facing page to that of the descriptions to which they apply. The illustrations vary in quality—there are some good colour plates, but a number of the black and white photographs, some necessarily reproductions of lithographs rather than actual specimens, are not as clear as they might have been.

This handbook will no doubt prove as valuable to the research worker as to the amateur conchologist, for the text, which is written as far as possible in non-technical language, loses nothing thereby in accuracy. Essentially a monograph of shells, one must not expect to find descriptions of the soft parts of the animals, and by the same token the section on cephalopods is restricted to a description of the paper nautiloids.

N.A.H.

W.R.G. Atkins.

OBITUARY

W. R. G. Atkins, C.B.E., O.B.E.(Mil.), Sc.D., F.R.I.C., F.Inst.P., F.R.S.
1884–1959

William Ringrose Gelston Atkins was appointed Head of the Department of General Physiology at the Plymouth Laboratory in February 1921 at the age of 36 having already at Trinity College, Dublin, applied widely the methods of physics and chemistry to the problems of biology, particularly botany. He was very well equipped to study the physics and chemistry of sea water as an environment for marine life. He served with great distinction at Plymouth, apart from the years of the Second World War, until he retired from the staff in March 1955 and enjoyed only four years of leisure before his death on 4 April 1959.

Atkins may be said to have borne the same relationship to chemical oceanography that V. M. Goldschmidt did to geochemistry. Each saw the problems of the waters or of the rocks broadly, drew on all the apparatus of research available in their day and founded each a new branch of science. They became close friends, mainly by correspondence and cross-fertilized each other. They differed in temperament, whereas Goldschmidt founded schools, Atkins preferred to work with his own hands or with those of his trusted assistants, Mr F. J. Warren and Miss Pamela Jenkins (Mrs L. Hummerstone). The greater part of his sea work was done on the 'Salpa', described when she arrived a few months after Atkins himself, as a powerful sea-boat and much more capable of facing rough weather than her predecessor. Powerful for her time she may have been but uncomfortable she certainly was, to an extent which those who work on our present vessels may find it hard to understand. It was on this ship that so much of Atkins's work, which became classical, was carried out. Her master, Captain Vivian Lord, was an individualist like Atkins himself. Each held the highest regard for the other for their personal integrity and competence at their respective jobs.

The chemical study of the sea as a biological environment started in Germany but the analytical methods of the day were not equal to the task. Matthews at Plymouth had introduced methods of improved accuracy but too slow for the considerable surveys which were necessary. Atkins's great gift was to realize the value of new techniques and then with great energy and care to apply them to problems which he was the first to define clearly. The credit for the first effective application of colorimetric, or as we prefer to say to-day, absorptiometric chemical analysis to oceanography is his.

He formulated clearly the problems of the biological productivity of temperate seas and started, following Benjamin Moore, by studying the carbon cycle, using measurement of pH as his tool. His results were clear-cut but he quickly realized that the answers he sought could be more surely obtained by studying phosphate. This he achieved by applying Denigès's colorimetric method to sea water. His technique was simple but effective and could be used on ocean-going research ships. During the years that followed he devised methods for a number of other constituents of sea water of biological importance, and applied them extensively.

Atkins quickly saw that production in the sea depended in equal measure upon the availability of nutrients and upon a sufficiency of light. As early as 1924 he entered upon a famous partnership with Dr H. H. Poole of the Royal Dublin Society which combined two acute minds with different gifts and opportunities to attack the intractable problem of the manner, the extent and the consequences of the penetration of light in the sea. As joint authors they wrote over forty papers, many of which have become classics. They found that though the photo-electric cell was much the best tool for the job, the early models could be treacherous. Much meticulous work was carried out to track down sources of error, many still with us, so that young men entering this field of research would be well advised to read for themselves how these sources of error were recognized and overcome.

One result of this intimate knowledge of photo-electric cells and their failings was that in his other main field of study, absorptiometric analysis, he remained to the end of his days an advocate of visual methods and rejected photo-electric methods. Possessed himself of exceptional powers of colour discrimination and memory he found it hard to realize that few shared his gifts or that the fatigue and failings of a modern photo-electric cell might be less serious than those of most human eyes. He was ever ready to give from his wide experience and one consequence was the application of his work in terrestrial environments, as in soils and woods all over the world.

For many years he continued work on the preservation of nets and ropes which developed from his earlier work in Egypt on fabrics. This was typical of the way in which he applied his discoveries in one branch of science to the problems of another.

An account of the many honours he received and of his work at Dublin and elsewhere during the two world wars will be found in the Obituary Notices of the Royal Society and in *Nature* (2 May 1959).

Atkins was a man of strong and forthright character, often stern in his support of causes which he felt to be just. He expected high standards of experimental competence and scientific integrity from his staff and from workers visiting the Laboratory. He was a very kindly man with a strong social conscience. Much of the good work that he did was known only to those who were very near to him. In his private life he was devoted to home and garden. To Mrs Atkins and their married son, all who knew them—and they were many—will extend deep sympathy.

L. H. N. COOPER

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SOME THEOREMS AND PROCEDURES IN SHALLOW-WATER OCEANOGRAPHY APPLIED TO THE CELTIC SEA

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(Text-figs 1–5)

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Twenty years ago the Plymouth Laboratory investigated the spawning of mackerel and pilchard in the Celtic Sea. The physical background for their work, which the late Dr G. A. Steven and Mr P. G. Corbin sought, could not be provided since waters with similar temperatures and salinities evidently had very different physical and biological histories.

Thus any study of the physical and chemical oceanography of the Celtic Sea, as of other waters around Britain, is an industrial rather than a fundamental research. Answers are needed for practical ends so that an imperfect answer today may be as useful as a thorough understanding tomorrow. In such circumstances oceanographers fall back on intuitions, which they cannot defend, to amplify inadequate observation. Since my own views about the Celtic Sea were so largely intuitive they have never been published. In 1948, an attempt at rationalization was made, much in the form to be presented here. Some of the theorems were used as working hypotheses when the 1950 programme was designed and proved compatible with the observations (Cooper, 1960, and in preparation), others remained shelved awaiting opportunity for tests which have never come. Now that 9 more years have passed, these theorems may help to build a bridge with findings in the same area by the Lowestoft Fisheries Laboratory. No more is claimed than that no theorem is in conflict with observations some of which will be published in a paper now in preparation.

In order to understand the water circulation better, it is essential to appreciate the pattern of winds over the area and what they are likely to do to the sea, to understand the effects of the physiography of the sea bed and of the neighbouring land on currents, and to eliminate the effect of latitude on temperature. These problems have been examined and some conclusions drawn. Their importance is that if they are indeed true, then they may always be true and applicable on occasions when only few observational records are available.

PATTERNS OF WIND-INDUCED CURRENTS

There is little doubt that west of a line drawn from Waterford through the Scilly Isles to a point 30 miles west of Ushant and within a line drawn 20 miles north-east and east of the continental edge, the currents are mainly wind-induced and are as variable as the winds. Rarely will the distribution of mass have time to approach equilibrium with the wind stress before this changes in strength and direction. This failure to reach an equilibrium state may account for failure during work spread over 20 years to find a satisfactory fit between a dynamic approach to the whole region and the information given by a study of nutrients and plankton indicators. Now that geometrical models of limited scope have been devised, short-lived equilibrium states may be recognized and studied with more hope of success.

Any steady wind over deep water should produce, in accordance with Ekman's (1905) theory, a surface current 45° to the right of the wind direction. In shallow water unrestricted by any land mass this angle will be smaller the less the depth of water and the stronger the wind. In summer the thermocline acts as a false bottom so that above a thermocline or above any discontinuity layer the current will run more nearly in the direction of the wind. In Fig. 1 the system of currents that should result in the Celtic Sea and English Channel from winds from six directions are presented for winter conditions.

Over a fairly small sea area such as the Celtic Sea, it should be possible to compute the torque exerted on the surface of the Celtic Sea from wind records at coastal observatories. For the 5 weeks preceding the cruise of April 1950, the pattern of winds at three well-placed exposed meteorological stations has been examined, viz. Scilly, St Ann's Head in Pembrokeshire, and Valentia in County Kerry. The period has been broken down into five parts each with a well-defined wind pattern (Table 1) and then summed up for the whole period. Vector addition has been used.

The direction of the mean wind measured over the whole 5 weeks at St Ann's Head was over 30° greater than at Scilly—251° as compared with 218°. Moreover, a similar difference showed up on each of the five shorter periods with winds from east through south to west-north-west. However, the difference in wind direction may be due to differences of latitude, or

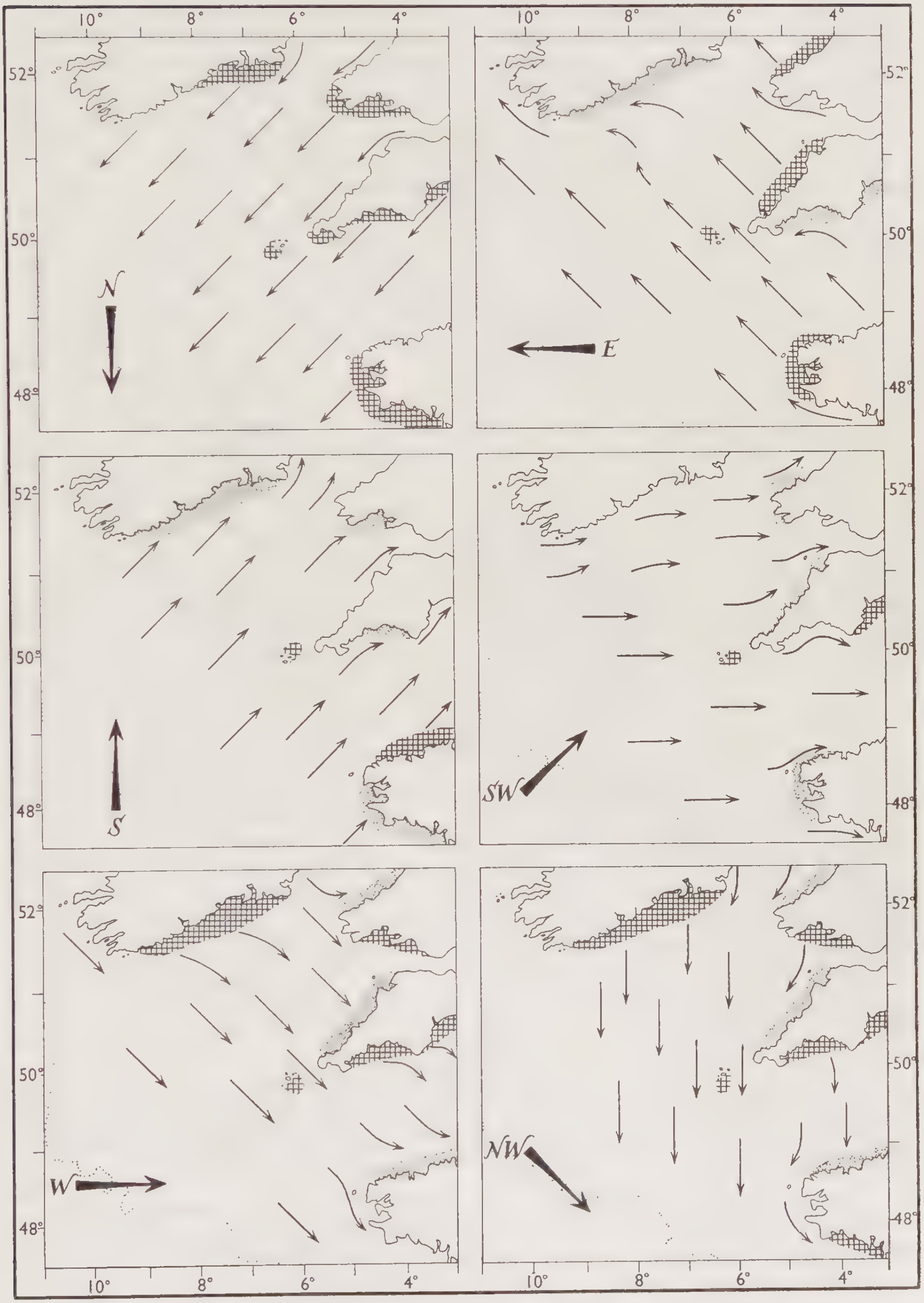

Fig. 1. Hypothetical system of surface currents induced in the Celtic Sea by winds in winter. The direction of the wind is shown by the heavy arrow in the bottom left-hand corner. Areas where upwelling should be favoured are cross-hatched. Areas where water must escape by sinking or by strong coastal flows are stippled.

regional topography, or the siting of the anemometers. Consequently the possibility that a cyclonic wind torque over the approaches to the Bristol Channel is commonplace needs further study.

Again, since the wind blows along straight lines only in the warm sector of a cyclone, and not always there, none of the current systems predicated in Fig. 1 can be initiated everywhere at the same time. Cyclonic winds must produce a cyclonic component of the current system.

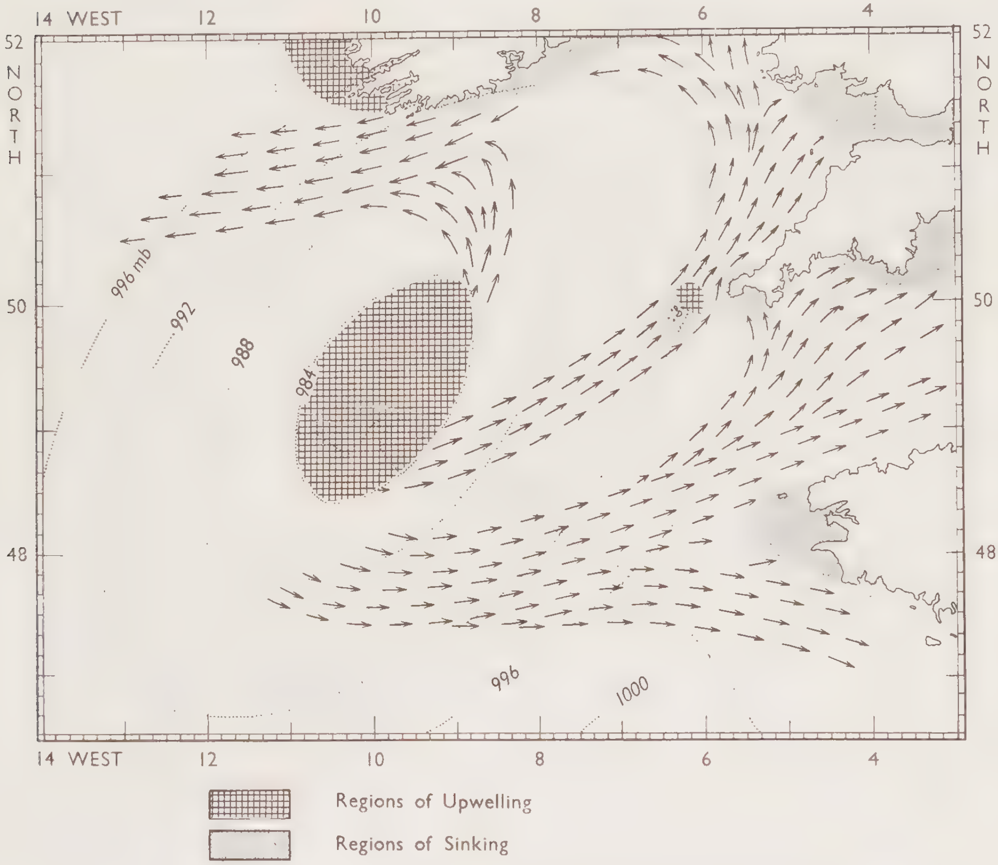

Fig. 2. The meteorological situation at 06·00 h on 6 January 1951 is used to illustrate the torque and resulting surface currents produced by a cyclonic depression centred over the Celtic Sea. Even if the centre passes at some distance, a similar pattern may be often resolved. Shading as in Fig. 1.

When an atmospheric depression lies over the Celtic Sea the distribution of air pressure (dotted isobars) is of the form observed at 06·00 h on 6 January 1951 (Meteorological Office, Daily Weather Reports) (Fig. 2). At sea level the resulting cyclonic wind was blowing across the isobars inwards towards the centre. Since the surface water current at every point would be initiated to the right of the surface wind direction, the surface currents will diverge a few degrees to the right of the isobars. Under the centre of the depression, a vortex will tend to form, accompanied by upwelling and diverging surface currents. In compensation, bottom water must converge on the vortex. Its course will be much influenced by the bottom topography.

The land constrains the current system absolutely so that the atmospheric pressure system on the morning of 6 January 1951 would have initiated a current system such as that in Fig. 2.

Such an atmospheric pressure distribution ought therefore to produce a torque on the sea surface, and it is this over-all torque and not the wind direction and strength at any one position which may produce the cyclonic circulation of the Celtic Sea.

TABLE 1. INTEGRATED MEAN WIND DIRECTIONS AT THREE METEOROLOGICAL STATIONS BORDERING THE CELTIC SEA

Period 1950	No. of observations	Mean wind direction: St Ann's Head	Mean wind direction: Scilly	Mean wind direction: Valentia	Difference: St Ann's Head – Scilly
14 March, 00.00 h–24 March, 06.00 h	42	233½°	202°	179°	+31½°
24 March, 12·00 h–29 March, 12.00 h	21	118°	66°	134½°	+52°
29 March, 18.00 h–5 April, 06.00 h	27	306½°	281°	300°	+25½°
5 April, 12.00 h–7 April, 24.00 h	11	205½°	164°	193°	+41½°
8 April, 06.00 h–17 April, 24.00 h	40	292°	278°	283°	+14°
14 March, 00.00 h–17 April, 24.00 h	141	251°	218°	226°	+33°

The centre of a cyclonic depression passes over the Celtic Sea not very often and when it does it stays there not very long. Occasions when a simple circulation such as that in Fig. 2 may be initiated may be rare. Nevertheless, when a depression passes over or near the British Isles, and that is often, a cyclonic torque may be resolved from the depression and will be operative over the Celtic Sea as a whole and it is this torque rather than a south-westerly wind off Ushant or a north-easterly one off southern Ireland which produces the observed circulation. It may therefore often prove necessary to combine two or more of the charts in Fig. 1 for different parts of the area to evaluate a real occasion.

In summer when the thermocline forms, the arrows in Fig. 1 all require to be rotated in an anticlockwise direction. A study of the currents around Ushant (Cooper, 1960) has shown that just such a change in current direction occurred there after the thermocline had formed in the summer of 1950. If the conclusion may be generalized, as probably it may, it could be of importance for studies on the seasonal drift of fish eggs anywhere.

VORTEX LANES IN THE SEA AND PLANKTON PRODUCTION

Beneath the centre of a depression a vortex will be created in the sea to a considerable depth. Under extreme conditions the water in this vortex may be carried upwards into the air as a waterspout. In winter the vertical column approaches homogeneity so that the vortex can do little by further mixing the water column but, even then, it may have an effect by disturbing bottom deposits. When the water is stratified, as often in summer, the passage of a deep depression in the atmosphere may produce, by upwelling in the sea beneath it, a 'vortex lane' of surface enrichment. Along this vortex a summer outburst of phytoplankton may possibly ensue.

The upwelling vortex in shallow seas is likely to create considerable disturbance of light bottom deposits and occluded dissolved products of regeneration and to suck these towards the surface. A vortex lane should become characterized by a high content not only of total phosphorus, silicate and bacteria but also of chemical substances which affect the growth of plants and animals. This phenomenon should be especially marked over mud bottoms. Phytoplankton outbursts in a vortex lane are therefore likely to consist of a few species which find conditions especially favourable. Similarly animals which spawn into a vortex lane will find exceptional conditions (cf. Wilson, 1951; Cooper, 1951) which may be favourable to some. The zooplankton which subsequently develops may possibly include characteristic indicator species.

THE EFFECT OF THE PHYSIOGRAPHY OF A LAND MASS, SOUTHERN IRELAND

The currents in the northern Celtic Sea may be much influenced by the physiography of southern Ireland. Between Dungarvan Harbour and Cape Clear the coast runs E.N.E.–S.S.W. Winds from south-south-west will tend to initiate currents along the coastline (cf. Fig. 1). Winds between south-west and north-west will tend to cause a similar coastal current but with an off-shore set at the surface.

The main drainage of south-western Ireland runs in deeply cut valleys from west to east or vice versa (Fig. 3). Although several of the original west–east rivers have been captured by others which have cut south across the ridges, the original valleys will channel surface winds from between north-west and south-west, so that they reach the coast in the neighbourhood of Waterford, Dungarvan and Youghal harbours more nearly from due west. There they should tend to produce a series of parallel off-shore currents setting between east-south-east and south-east. Waterford Harbour not only receives the Suir from the west, connected by a low watershed to the valley of the Shannon estuary, but the Barrow which has cut for itself a deep valley running for 50 miles practically due south along the meridian 6° 57′ W. This will similarly channel northerly winds which, whilst they blow, should initiate a current setting south-south-west or south-west off Waterford Harbour.

These are upwelling situations likely, when the wind is favourable, to initiate productive centres, particularly off Waterford at about 51° 40′ N., 7° W. This effect of physiography has been used by Cromwell (1956) to explain the productivity of the Gulf of Tehuantepec on the Pacific coast of southern Mexico. There strong or gale force northerly winds blow through the low and narrow Tehuantepec Pass on to the Gulf to produce an upwelling situation.

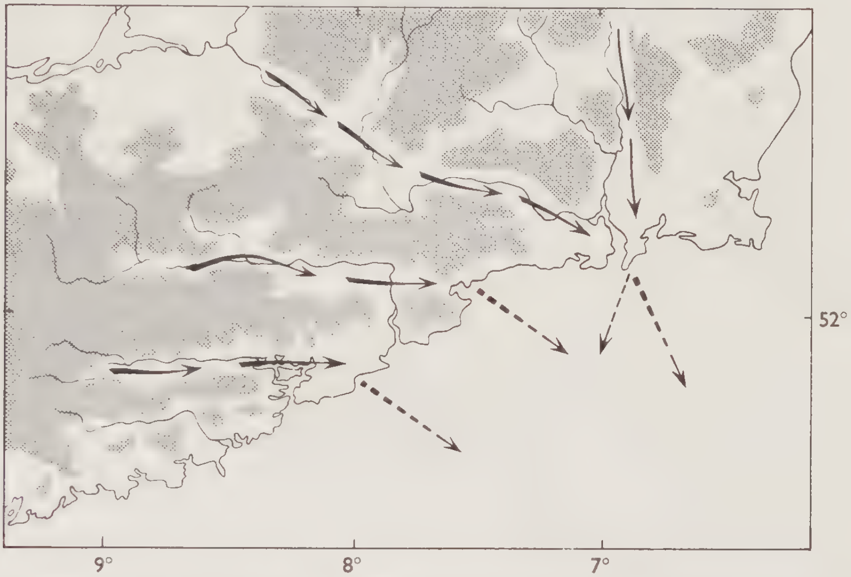

Fig. 3. To illustrate the effect of the prevailing westerly and south-westerly winds combined with the physiography of southern Ireland on currents and upwelling in the northern Celtic Sea. The effect of northerly winds channeled by the Barrow valley is also shown.

The prevailing winds of southern Ireland, which often blow with gale force, should therefore tend to create coastal currents towards the east often trending away from the coast.

To oppose this current system, the Coriolis force operating on the main cyclonic circulation system of the Celtic Sea and favoured by the light coastal belt of water of low salinity will tend to create a coastal current setting west or west-south-west along the length of southern Ireland. Moreover, the two opposed tendencies are produced by much the same winds and may therefore be in frequent conflict. The conflict can only be relieved by a current setting south away from the coast and this seems most often to occur in 7° W., the longitude of Waterford Harbour. This may be pictured as a large-scale rip current (Shepard, 1948). The analogy should not be pressed too far and the term ‘rip’ should not be transferred. Such a current shows the site of a surface divergence. A cyclonic wind system may therefore produce an anticyclonic current south of County Cork which may force the main cyclonic circulation into a narrow ellipsoidal figure lying east of 8° W. long.

The main cyclonic eddy is much the greater and contains much more water and momentum than the County Cork anticyclonic current. Consequently as soon as the westerly or south-westerly winds die down the main cyclonic current should become dominant, spreading westwards, becoming more nearly circular and creating a westerly coastal current of the usual type with the land of southern Ireland on its right.

The south-going current frequently found in about 7° W. long. thus may arise by synthesis from two or three water masses, one the rather brackish, nutrient-poor and, in winter, cold water mass which has passed Carnsore Point as part of the main Celtic Sea cyclonic circulation and the other the salter, and in winter, warmer water mass contributed from the west by the County Cork anticyclonic current and by upwelling during northerly gales. It was this mixed water which in April 1950 provided the main recruitment of salt water ultimately as a bottom current into the inner Bristol Channel (paper in preparation).

The position of this current is controlled by the physiography of the land, by the direction and strength of the wind and only in small degree by the distribution of mass in the water. Once in being, a redistribution of mass in the current must occur in accordance with dynamic theory.

Under the physiographic and physical conditions which produce it, this current would be forced into the eye of the wind so that surface movement should be retarded. Maximum current should flow in mid-water or near the bottom. Also the direction of surface movement is likely to differ markedly from that near the bottom. Surface movement should trend south-west, mid-water south-east, and bottom movement east towards the Bristol Channel. The Ekman spiral would seem not to apply to such a current forced to flow against the direction of the wind. Under such conditions no help in sketching its course is to be expected from charts of dynamic height anomalies (geopotential topographies).

THE NATURE OF THE BOTTOM DEPOSITS OFF SOUTHERN IRELAND

The topography of the bed of the Celtic Sea has been contoured and described by Robinson (1952). Matthews (1914) pointed to the importance of the weak tidal streaming and small scour in favouring deposition of mud between about 51° N., 6° W. and the coast of County Waterford.

Much information as to the nature of the bed of the Celtic Sea is given on old charts published privately and by the Hydrographic Office. Off the south coast of Ireland in depths of about 35–40 fm. there are many references to 'mud' and 'ooze'. Along the south coast of Cornwall, which in its physiography and exposure to wind has much in common with southern Ireland, no such deposits of mud and ooze were reported nor, indeed, are found by our research ships.

Again, off southern Ireland, there are many records of 'muddy stones', 'muddy gravel', or 'mud' with 'stones' nearby at a similar depth. The picture one has is of an area of what on land would be called boulder clay, deposited during the southernmost extension of glaciation in Ireland. If so the stones have lain there uncovered for at least 10,000 years. Much of the mud, therefore, can be no more than a veneer. If the area was one of strong unidirectional residual currents, as the south coast of Cornwall seems to be, detritus would be swept away to be deposited somewhere else. It would not collect even as a veneer.

If this interpretation as an area of boulder clay overlain by a veneer of mud is correct, we have an equilibrium system: (*a*) the area is one of weak currents which enable mud to be deposited or of horizontal or vertical eddies which tend to concentrate detritus to settle on the bottom beneath, but (*b*) the area is also one where the muddy deposits are creamed off probably intermittently as the result of storm action to be redeposited further south or west. Coring work in this region is badly needed.

A solution may be approached in two ways. Detritus, even organic detritus, is heavier than water, and so tends to settle on the bottom. Our prevailing winds tend to produce an upwelling situation along the south coast of Ireland. Detritus caught up in such a situation will tend to undergo a cyclic movement. Material inshore near the bottom may rise with the upwelling water to be carried seaward in the surface offset. From this it would settle into the deeper water some of which will be drawn back towards the site of upwelling.

Although by itself this mechanism would be insufficient to build up a muddy deposit, it would seem to be a necessary component of one that might. Its biochemical implications need also to be considered. If the detritus should consist of a pure clay mineral it would have no nutrient value and would reduce the amount of light available for photosynthesis. Its effect would be adverse. The clay might carry adsorbed materials which have value to plants. The important part of the detritus, sometimes called seston, would be organic material resulting from death and defaecation and capable of yielding breakdown products essential for the subsequent success of plants and animals in the water. Such organic detritus, only slightly heavier than water, cycling in this way, is particularly likely to provide an explanation of the richness established along the south coast of Ireland by the Lowestoft and Plymouth research vessels in 1958–59.

This mechanism would also favour the concentration of zooplankton which undergo vertical migration from surface to bottom. It would, however, do them no good unless they found food to live on.

This argument would apply equally to much of the south coast of Cornwall, particularly off the Helford River. I know of no evidence for it there. There is, however, a second line of argument which complements the first.

In general, in the northern hemisphere, the outflow of rivers tends to build up a zone of brackish coastal water which, except sometimes at the time of minimum temperature, creates a band of light water which flows with the coast on its right. Along the south coast of Ireland, this current would flow from east to west. However, the direction of the prevailing winds combined with the physiography of the area may, as we have seen, require a current along this coast in the opposite direction, west to east. Evidence for its existence in April 1950 will be produced in a later paper. When these tendencies cancel each other to produce no residual current in a region where tidal currents are weak, the load of detritus may be dropped.

At the Daunt light vessel off Cork Harbour, the table of the tidal stream given on Admiralty chart no. 2049 bears this annotation: 'Wind has so much effect on the direction and rate of the tidal streams at this position that the above table can only be looked upon as approximate and the stream may sometimes be found running even in the contrary direction to that given for any hour in the table'. South of the Daunt light vessel Imray's old chart shows many entries for mud.

By combining the two arguments the difference between the bottom deposits off the south coasts of Ireland and of Cornwall, which otherwise have so much in common, may be explained.

A study of these muddy bottoms may, therefore, for several reasons have a proper place in fisheries research.

THE EFFECT OF THE LABADIE BANK

The Labadie Bank, 20 miles long but only 3 miles wide, extends in a direction south-west by west and lies about 60 miles off the Irish Coast. It rises 40 m from the sea bed in 110 m and is connected by deeper spurs with the Cockburn and Great Sole Banks lying more than 60 miles to the south-west. This system of banks may exert some control over currents in their neighbourhood and tend to make them conform to a north-easterly–south-westerly pattern.

The Bank lies athwart the general south-easterly and southerly trend of the County Cork anticyclonic current. Both the Coriolis force and the pressure of the main Celtic Sea cyclonic circulation tend to turn this current to the right or south-west in line with the constraint imposed by the Bank. On many occasions the Labadie Bank may provide the southern limit of the County Cork anticyclonic system.

The degree of permanence of this anticyclonic system has not yet been assessed but it is likely that on occasion it may last long enough to become markedly enriched from the mud deposits of the Labadie area (Cooper, 1951) and off the south coast of Ireland, not only with inorganic nutrients but with growth-affecting substances as well. Then distinctive chemical composition may lead in time to the development of characteristic biological indicator species.

THE EFFECT OF THE SCILLY ISLES

The Scilly Isles comprise a few small inhabited islands and a large number of rocks rising from an elevation of the sea floor about 11 miles long and 5 miles wide. The surrounding sea floor lies at 70–80 m, whereas the depth of water within the islands ranges from 15 to 45 m. There can be but little land drainage to affect the density of the water.

When air temperature is below sea temperature, as frequently in autumn and winter, the water within the island group will be cooled further and become heavier than in the adjacent sea (Cooper & Vaux, 1949). It will therefore sink and flow out by the deepest channels, North Channel and Broad Sound on the western side of the Isles. To replace this loss, surface water will be drawn in through the many surface channels so that a cyclonic current will be created round the Isles (Sandström, 1918, fig. 41*a*).

When air temperature is above sea temperature or much solar radiation is being received, the sea surface will warm up everywhere but, due to the rugged bottom topography of the Isles, vertical mixing there would be expected to extend deeper than in the adjacent open sea. Although the surface water may become slightly cooler, the vertical water column as a whole should become lighter than outside. A rising centre has come into being so that there will be a tendency for water to be drawn in through the two deepest channels and ejected at some depth between the surface and the depth of the thermocline outside.

These conditions are more complicated than those associated with cooling but the net effect would seem to be to create a divergent anticyclonic current round the Isles at or just above the level of the thermocline.

It is not considered that these trends will ever be dominant but that they will modify currents near the Isles due to other causes. Carruthers, Lawford & Veley (1951) have found that at the Seven Stones Light Vessel, 9 miles E.N.E. of the islands, the current sets on the average towards 110° true. On this view during cold weather this current should set more nearly east, whereas in warm sunny weather it should set more nearly south. When such fluctuations are actually observed they may need to be interpreted not in terms of a major change in the current system of the Celtic Sea, but as no more than a local effect due to the presence of the Scilly Isles.

ELIMINATION OF THE LATITUDE EFFECT IN PLOTTING TEMPERATURES

In these investigations charts and sections of temperature did not at first prove helpful. It is not easy to deduce currents with a meridional component from plots of temperature because as a current moves southward it is warmed by insolation to a greater extent than it loses heat by radiation and evaporation. Such a current is also continuously warming up by lateral mixing with warm water through which it flows.

When, as in our April 1950 cruise, the lay-out of the sections is latitudinal, it is worth while to eliminate the effect of latitude. Calculating along the fiftieth parallel, as shown in Table 2, the effect of uneven spacing of the stations is eliminated. Between Lands End and a point north of Scilly, stations were 7 miles apart, whereas to the westward the interval was 30 miles. Proper weight is given to the length of the section which each station must represent.

TABLE 2. MEAN TEMPERATURES ALONG 50° N. (FIRST APPROXIMATION) 10·17°

Station	Lat. (°N.)	Long. (°W.)	Limits represented by station (long. °)	Minutes of long. ($\Delta\lambda$)	Observed temp. °C (T)	$\theta = T - 10°$	$\theta\Delta\lambda$	Temp. correct to 50° 00′ N.
			9° 15′					
20	49° 57′	9° 06′		20′	9·99	−0·01	−0·20	9·97
			8° 55′					
21	49° 56′	8° 45′		17′	10·15	0·15	+2·55	10·12
			8° 38′					
22	49° 58′	8° 31′		25′	10·17	0·17	+4·25	10·16
			8° 13′					
23	50° 03′	7° 55′		30½′	10·33	0·33	+10·07	10·35
			7° 42½′					
24	50° 00′	7° 30′		29½′	10·20	0·20	+5·90	10·20
			7° 13′					
25	49° 58′	6° 56′		28′	10·16	0·16	+4·48	10·15
			6° 45′					
26	50° 04′	6° 34′		17½′	10·20	0·20	+3·50	10·23
			6° 27½′					
27	50° 04′	6° 21′		9½′	10·10	0·10	+0·95	10·13
			6° 18′					
28	50° 04′	6° 15′		7′	10·08	0·08	+0·56	10·11
			6° 11′					
29	50° 04′	6° 07′		7½′	10·17	0·17	+1·28	10·20
			6° 03½′					
30	50° 04′	6° 00′		7′	10·08	0·08	+0·56	10·11
			5° 56½′					
31	50° 04′	5° 53′		7½′	10·22	0·22	+1·65	10·25
			5° 49′					
32	50° 04′	5° 45½′		7′	10·24	0·24	+1·68	10·27
			5° 42′					
			213′				37·03	

$$\theta_{\text{mean}} = \frac{\Sigma\theta.\Delta\lambda}{\Sigma\Delta\lambda} = \frac{37\cdot03}{213} = 0\cdot17^\circ.$$

Assuming that all stations lay precisely on the fiftieth parallel the calculation gave as a first approximation a mean latitude temperature of 10·17° C. However, some stations deviated 4′ from the parallel. A similar calculation for latitude 49° 30′ N. had given the mean temperature for that latitude as

10·48° C. It was therefore possible to apply a correction of 0·01° per minute of latitude to correct each observed temperature along each latitude to 50° 00′ N. or to 49° 30′ N. precisely. This refinement increased the mean latitude temperature along 50° N. by a mere 0·01° C. This figure was used for further development.

By similar means the mean temperature was computed for other lines of latitude where enough observations were available (Table 3, column 4).

In order to use all the available observations and to distribute error and random deviations, it was assumed that the rate of decrease of temperature was linear with latitude. A least mean square of calculation then gave the relation

$$T = 10{\cdot}46 - \frac{0{\cdot}712}{100}(\Phi - 2970),$$

where Φ is the station latitude and 2970 is the latitude 49° 30′, each expressed in minutes of arc.

The final column in the Table shows the mean temperature for latitude computed in this way.

For a depth of 10 m, at each of the 57 stations worked during the cruise of April 1950, the latitude temperature was then computed. Finally, the difference of each observed temperature from the computed latitude temperature was evaluated and plotted on a graph as in Fig. 4. The information will be used in a paper in preparation.

TABLE 3

Lat. (°N.)	Limits of long. (W.)	No. of observations	Mean temp. for lat.: Observed on lat. only	Mean temp. for lat.: Mean square calc. from whole area
51° 20′	5° 05′–9° 00′	5	9·65	9·68
51°	4° 45′–9° 15′	5	9·87	9·82
50° 35′	5° 20′–9° 05′	6	9·98	10·00
50° 00′	5° 42′–9° 15′	13	10·18	10·25
49° 30′	4° 45′–9° 15′	9	10·49	10·46

It will be seen that, strictly speaking, the development has added nothing which could not have been deduced by careful drawing and study of a conventional chart of isothermal contours. However, to use a simile from electronics, the required information has been raised above the level of the background noise. The enclave of water north of Cornwall shows this well.

The technique has another application. One often needs to decide whether the sea at any time is warmer or colder than at some other time. Inevitably oceanographic observations are untidy and heterogeneous. Elimination of the 'Latitude Effect' should enable a lot of scattered observations to be summarized in a compact and convenient equation in standard form and to be used for practical ends. One such is fog forecasting where the forecaster

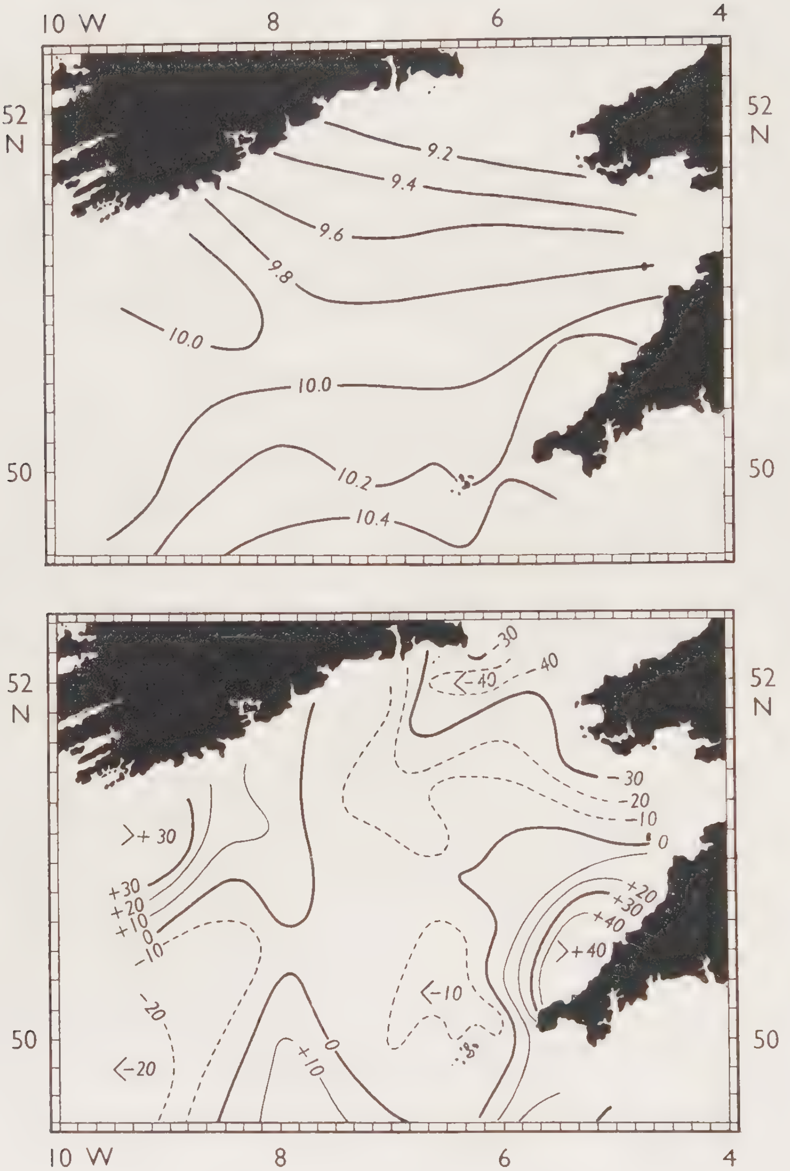
10 W
8
6
4
52 N
50
9.2
9.4
9.6
9.8
10.0
10.0
10.2
10.4
-30
<-40
-40
-30
-20
-10
0
>+ 30
+30
+20
+10
0
-10
-20
<-20
0
+10
<-10
+20
+30
+40
>+40

Fig. 4. Two ways of presenting sea temperatures in the Celtic Sea, 19–30 April 1950 at 10 m depth. Upper panel as conventional isotherms, lower panel as deviations from the latitude mean.

needs much more information that he is every likely to get for all of the time and all of the area for which he needs it.

In an investigation where observations have been made in a symmetrical pattern, the calculation may be much curtailed. One could proceed straight into a least-mean-square calculation using all the data. But if some of the stations are clustered, as in April 1950 around the Scilly Isles, bias would be introduced by this short-cut.

THE USE OF GEOPOTENTIAL TOPOGRAPHIES IN SHALLOW-WATER OCEANOGRAPHY

In common practice geopotential topographies are drawn only in oceanic areas where there is a probability of a level surface at a depth in which no motion may reasonably be assumed. The lead set by Harvey (1929) for shallow water work has been rarely followed.

In shallow seas there can be no level surface of no motion. Nevertheless, in our own shallow-water work in the Celtic Sea we have always drawn geopotential topographies and have found them to have diagnostic value. Any deductions which may be drawn must always be consistent with the continuity of conservative and semi-conservative properties of the water.

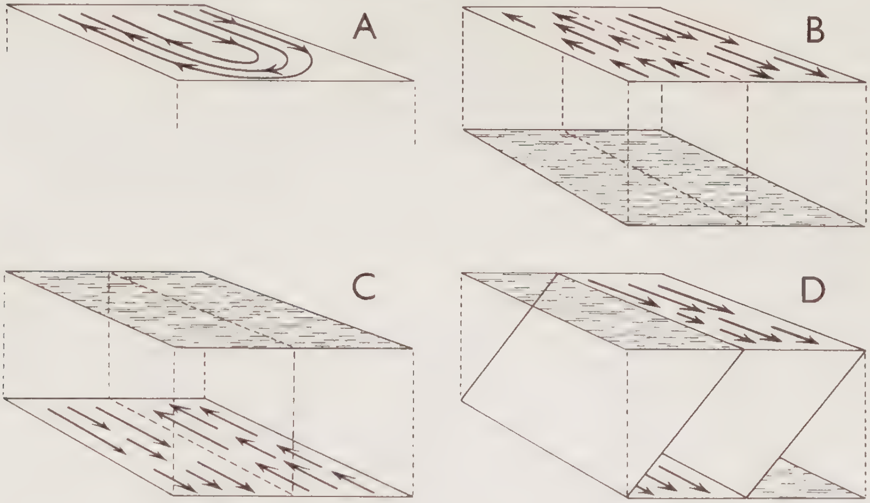

Fig. 5. Interpretations of a tongue in a geopotential topography.

Tongues on geopotential topographies (Fig. 5A) are usually interpreted as geostrophic surface flow along the isolines (Fig. 5B); similarly to geostrophic winds on a meterological isobaric chart. Occasionally, they may be interpreted as a precisely opposite bottom flow, the surface being considered a layer of no motion (Fig. 5C). There is, however, another possibility (Fig. 5D) which may often be important in shallow-water oceanography when water piled up against a coast by wind has to escape as a bottom or mid-water current flowing against the wind at the surface. In this the two halves of the geopotential topography may be interpreted oppositely, so that a picture emerges of a unidirectional current sloping from the surface where the conventional arrows face towards the tip of the tongue to the bottom where they face away from it. The maximum strength may well be in mid-water beneath the axis of the tongue.

Lateral mixing is usually considered as occurring across a more or less vertical boundary. Allowing for the vertical exaggeration of scale, the present interpretation of geopotential topography may require that the boundary between a current and its envelope of stationary water shall dip beneath the surface at an angle of only 1° or so with the horizontal.

Studies of eddy diffusion and eddy viscosity in such a situation take a different form when horizontal and vertical coefficients require to be replaced by oblique coefficients.

This theorem may be illustrated by the events in the Celtic Sea in April 1950, described in a paper in preparation.

SUMMARY

An attempt, made in 1948, to rationalize some intuitive views about the circulation of the Celtic Sea is here presented.

Using Ekman's theory, the surface currents in the partially land-locked Celtic Sea are suggested for six wind-directions. A means of computing the cyclonic torque of gales upon the Celtic Sea is tentatively proposed.

Passage of a cyclone over a sea area may produce a 'vortex lane' leading to enrichment of the surface with nutrients and productive conditions along the lane.

The physiography of southern Ireland combined with the prevailing or northerly winds is likely to produce an upwelling situation, particularly off Waterford where a large scale 'rip' current may develop. In addition to the main cyclonic circulation of the Celtic Sea, the prevailing winds may build up south of County Cork an anticyclonic eddy with the 'rip' current as a common boundary. The probable structure of this current is discussed.

The difference in the nature of the bottom deposits south of Cornwall and south of Ireland, regions with much in common, is considered in relation to the current régime and to biological productivity.

It is suggested that the Labadie Bank may affect the direction of currents, especially the intermittent County Cork anticyclonic eddy.

In both winter and summer it is suggested that events within the Scilly Island group may affect the currents in the neighbourhood, as at the Seven Stones Light Vessel.

A method is given of eliminating the latitude effect from a study of temperature in a limited sea area.

A profitable method of applying information from geopotential topographies in shallow seas is described.

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THE WATER FLOW INTO THE ENGLISH CHANNEL FROM THE SOUTH-WEST

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The Plymouth Laboratory

(Text-figs. 1–17)

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ON CURRENTS AROUND HEADLANDS

The physical oceanography of the shallow seas south-west of the British Isles is much influenced by the exchanges of waters around headlands between neighbouring areas of the sea. These are:

Bay of Biscay (south-west of Brittany)–*Ushant*–English Channel
English Channel–*Lands End*–Bristol Channel
Bristol Channel–*St David's Head*–St Georges Channel
St Georges Channel–*Carnsore Point*–Celtic Sea (south of Co. Waterford)

This paper discusses the first of these, the recruitment of water from south and west of Ushant into the English Channel. Exchanges of water around the other headlands, together with the recruitment into the English and Bristol Channels of 'western' or 'elegans' waters will be discussed in a further paper now in preparation.

Off the Island of Ushant (I. d'Ouessant) the coast falls steeply to a peneplain at about 110 m. Tides are very strong and the coastline very rugged. Twenty-five miles to the south the Chaussée de Sein (The Saints shoal) projects about 15 miles to seaward and must cause much mixing in coastal water which may flow northwards along the coast of Brittany towards Ushant. Here in summer the surface layers often become cooler and the deeper layers warmer than at corresponding depths in the sea to the westward. The distribution of mass is then such as to encourage the north-going current round the island to flow most strongly not at the surface but at a level around 20–30 m corresponding to that of the thermocline in the sea to the westward. If no other forces were operating the current at surface and near the bottom would flow southward from the English Channel into the Bay of Biscay.

However, in summer, after wet weather, land drainage contributes to the epithalassa and only slowly to the hypothalassa by vertical mixing against a density gradient. The density of the surface water becomes further decreased so that it should acquire a tendency to flow with the coast on the right. In general, summer or winter alike, rivers entering the sea in the northern hemisphere show a tendency to mix away to the right on the surface.

Dietrich (1950, 1951) applied a powerful thermodynamic approach to the circulation of the English Channel as a whole. This was based upon the increase in heat content of the water of the English Channel from its minimum in winter to its maximum in summer. The characteristic feature of thermodynamics is that it deals with the energy changes of a physical or chemical process without requiring a knowledge of the mechanism by which the process occurs. Correctly drawn conclusions are independent of hypothesis, a great advantage since such conclusions remain true even if some of our views about mechanism should undergo radical change. There are converse and very considerable disadvantages to a thermodynamic approach. Without help from other disciplines it cannot give information about mechanism. Consequently it is essential clearly to separate Dietrich's treatment into two parts, that which is strictly thermodynamic and that which is not so.

The unassailable part of Dietrich's paper (his Abbildung 4) is his conclusion that an area on the southern side of the Channel from immediately north-west of Ushant towards the north of the Cherbourg peninsula has a far greater range of temperature than can be accounted for by local exchanges of heat. There must be currents which bring much heat into the area or take it away.

As so often in physics and in physical chemistry, advance is fastest when thermodynamics can be complemented by another approach using, for example, kinetics or continuity of properties. Such methods admit of accurate study of detail, but first attempts at generalization, leaning all too heavily on analogy and intuition, may appear to conflict.

West of the meridian 3° W., the eastern limit of this study, there appears no conflict between my findings, as set out below, and the 13 figures published by Dietrich. Unfortunately those parts of Dietrich's interpretation which are not thermodynamic do not always agree well with mine. In particular, in stratified water north and west of Brittany, this investigation suggests that the residual current at depth sets to the left of that in the upper water. Hansen (1950) produced evidence with which Dietrich concurs that for tidal currents in similar circumstances mass transport tends towards the coast (i.e. to the right) in the bottom layers and away from it in the upper layers.[*]

THE USHANT CURRENT IN THE SPRING OF 1928

Let us now consider the current around Ushant in late winter and spring following prolonged heavy rain over France. Events in 1928, already briefly discussed by Poole & Atkins (1929, p. 318), illustrated the nature of this flow. Further information was published by the Conseil International (1929, *a*, *b*).

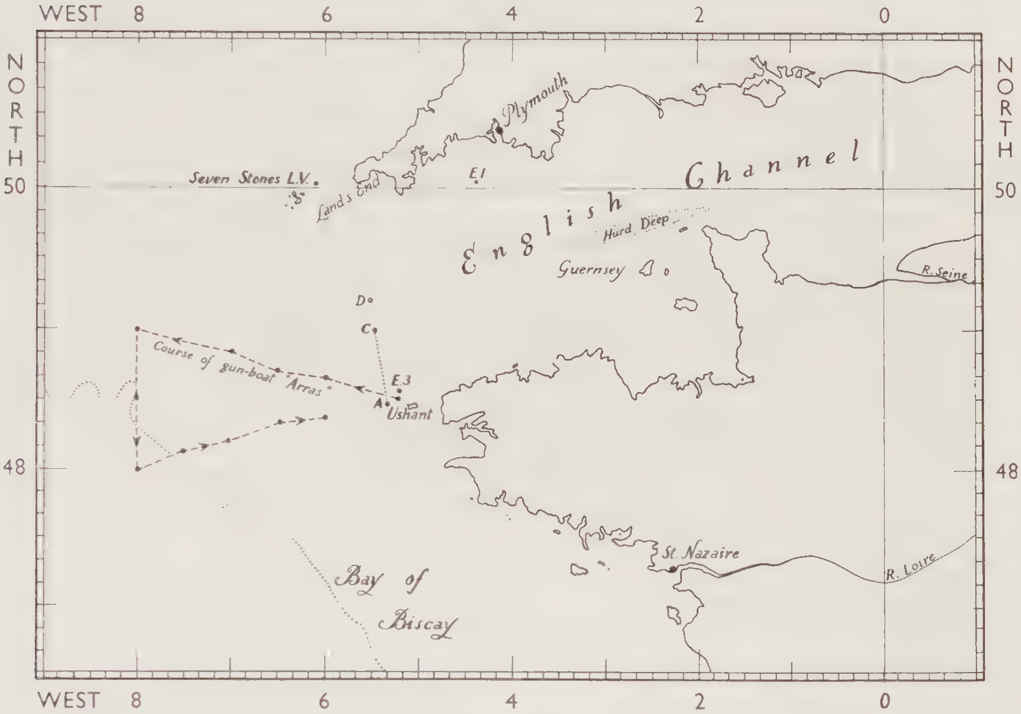
WEST
8
6
4
2
0
NORTH
50
48
Seven Stones L.V.
Land's End
Plymouth
E1
English Channel
Hurd Deep
Guernsey
R. Seine
D
C
E3
A
Ushant
Course of gun-boat "Arras"
St. Nazaire
R. Loire
Bay of Biscay

Fig. 1. A chart to illustrate the spread of run-off from the Loire watershed during the spring of 1928.

Early in that year very heavy rainfall occurred in the basin of the Loire, exceeding the normal for the 3 months January–March by 55%, whereas in England it was unexceptional. The heavy run-off spread northwards from the neighbourhood of St Nazaire (Fig. 1), so providing a label enabling its subsequent movement to be followed. Water of somewhat reduced salinity had begun to enter the English Channel by 22 February, the salinity at E3 being 35·01–35·09‰. By 24 March water of exceptionally low salinity (34·06‰)

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[*] Of Carruthers's (1927) drift bottle results, the few that are relevant to this enquiry support the views of Dietrich and of Hansen rather than my own.

was still present off Ushant at position *A*. In the following 11 days this brackish water spread out for over 30 miles north of Ushant (4 surface salinities on line *AC* 34·74–34·85‰). It had also reached eastward along the French coast to the Hurd Deep in 3° W.

By 5 May the stream of low-salinity water north of Ushant had widened by a further 13 miles to include the position *D* (five salinities between 34·41 and 34·88‰). On 9 May it was sampled by R.V. 'Salpa' at E3 when the uppermost 15 m had a salinity of 34·8‰.

Another week later on 15 May a triangle of stations was run by the French gun-boat 'Arras', her station 3 miles off Ushant revealing water having salinity 34·49–34·59‰ down to at least 50 m. However, at two stations on the sixth meridian (48° 22′ N. and 48° 38′ N.) no water less saline than 35·21‰ was present. To the westward of Ushant therefore this torrent of brackish water was not more than 30 miles wide. It may have been much less. To the northward of Ushant, it would seem that the momentum of the water mass was sufficient to carry it onward within an arc, centred on Ushant, of 40 miles radius. As the northward momentum fell away, the resulting mixed water mass moved up-Channel on the French side.

By 26–27 March the water had nowhere crossed the fiftieth parallel but in the next 5 days it did so. On 31 March it covered the whole of the line from Plymouth to Guernsey, and sometime before 19 April it had moved westward along the English side as far as station E1. During April and May the low-salinity water spread throughout the central and eastern parts of the Channel from which it was not displaced until October–November. By early June, however, the movement of low-salinity water past Ushant was over. No more was observed there.

The brackish water from off Plymouth approached Land's End from the east, arriving at the Seven Stones Light Vessel about 29 April, but was not there felt in full strength until 5 June. The main spate occurred during June and was over by 1 July. There were minor recurrences of less saline water (< 35·1‰) close into Land's End in the corner current until September but at the Seven Stones Light Vessel (50° 04′ N., 6° 05′ W.) this influence was not again detected. It is clear that the corner current around Land's End (50° 04′ N., 5° 43′ W.) was carrying a considerable volume of Loire and Seine watershed water even though the influence at the light vessel, which lies 14 miles west of the promontory, was undetectable. The Land's End corner current was quite narrow.

It is clear that during 1928 we experienced a hydrographical event of considerable magnitude, the whole of the English Channel being affected. It is probable, though not completely proved, that the Biscayan water diluted by run-off from the Loire watershed turned Ushant as a quite narrow current, not more than 30 miles wide and for most of the time probably much narrower. It took 10 weeks to reach Land's End at a rate of 3 miles a day by the route followed. When it did its tendency was to enter the Bristol Channel as a current snugging the headland and not to spread out to include the Seven Stones Light Vessel in its path. Added water alters both density and the consequent pattern of currents, particularly near Ushant. The spring of 1928 may therefore provide a pattern for the circulation of the western English Channel in spring only in years when rainfall over central and western France has been above average.

To understand the behaviour of any of these corner currents it is necessary to have very close stations in the offing and to have one as close to the headland as prudent navigation will allow.

It may not be chance that 1928 and 1929 provided very poor year-classes of hake. Hickling (1935) sought a correlation with the reduced run of the wind to the eastward during the breeding season, but the presence of much fresh water and a consequent pattern of currents may have played a part.

CURRENTS WEST OF USHANT IN THE SUMMER OF 1950

The English Channel and Celtic Sea were exceptionally thoroughly surveyed in the summer of 1950 (Conseil International, 1954) by the Lowestoft research vessel 'Sir Lancelot' and by our own vessel, 'Sabella'. Valuable information was also collected by R.R.S. 'Discovery II' and R.R.S. 'William Scoresby'. The vessels worked in informal but close association. Only observations relevant to currents west and north of Ushant are here considered (Fig. 3).

The important line of surface observations between Land's End and Ushant (no. 10) also requires special comment. This is operated on fortnightly schedules out and home by two ships which often pass each other in the mouth of the Channel. In the early months of 1950 serious discrepancies between temperature observed by each ship and those observed at the Seven Stones Light Vessel and by R.V. 'Sabella' were noted. By such comparison and by scrutinizing the times of observation, we have had good reason to reject observations from one ship for the whole year and from the second ship for the months of January, February and March. Observations from the second ship have been accepted for the following dates and are included in the isopleth (Fig. 2). It is understood that the Lowestoft Laboratory have arrived at a similar conclusion.

	Southbound	Northbound
(1)	11–12 April	17–18 April
(2)	23–24 April	29 April
(3)	7 May	12–13 May
(4)	22–23 May	29 May
(5)	3–4 June	10–11 June
(6)	17–18 June	24–25 June
(7)	1–2 July	14–15 July
(8)	22–23 July	2–3 August
(9)	16–17–18 Sept.	—
(10)	30 Sept.–1 Oct.	8–9 October
(11)	15 October	22–23 October
(12)	12–13 November	20 November
(13)	26–27 November	3 December
(14)	12–13 December	21–22 December

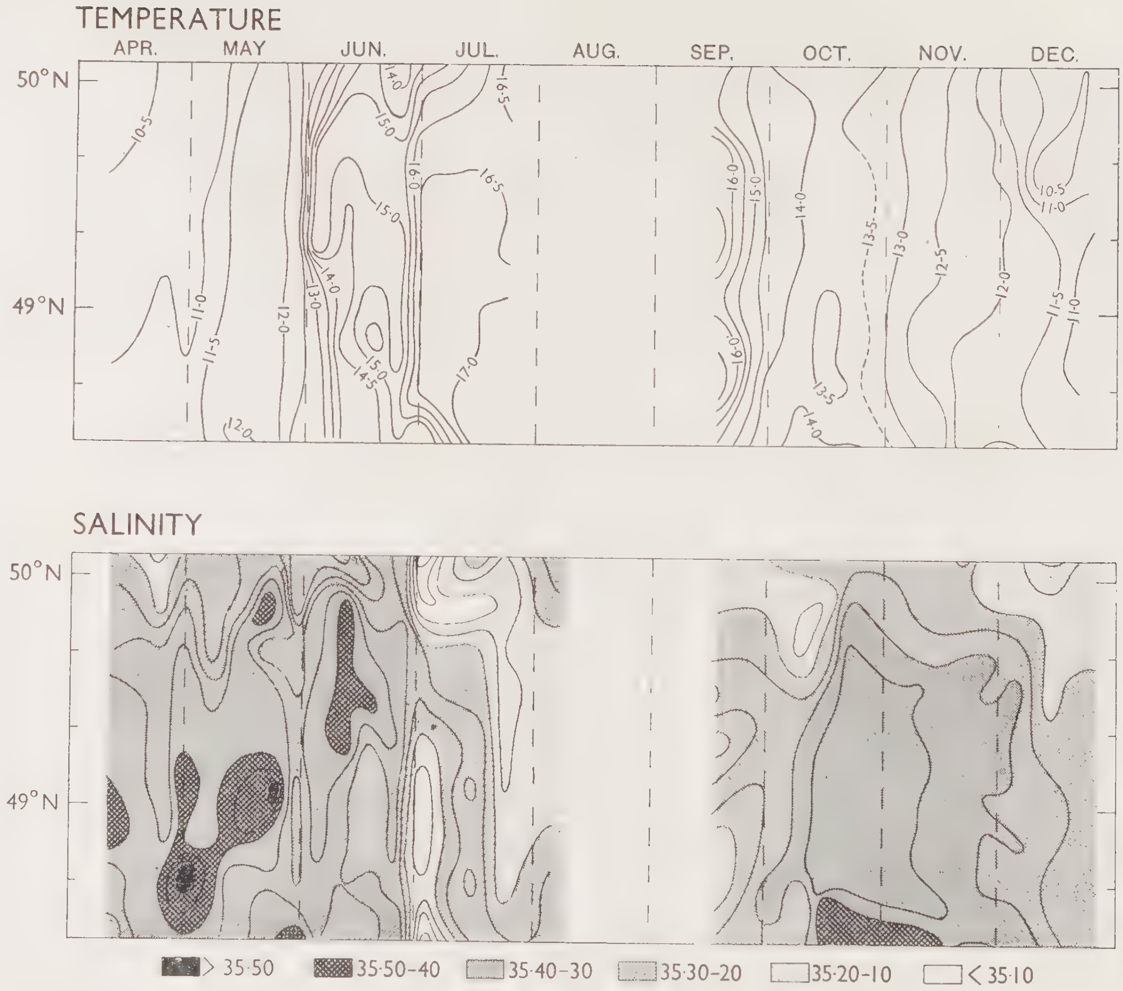

Fig. 2. Selected surface observations of temperature (°C) and salinity (‰) along line no. 10 between Land's End and Ushant. Time (April–December 1950) plotted against latitude.

'Sir Lancelot's' observations in August 1950

In August R.V. 'Sir Lancelot' worked a line of stations west of Ushant at even closer intervals than those of R.V. 'Sabella' in June and additionally made highly critical observations north of north-western Brittany (Fig. 3).

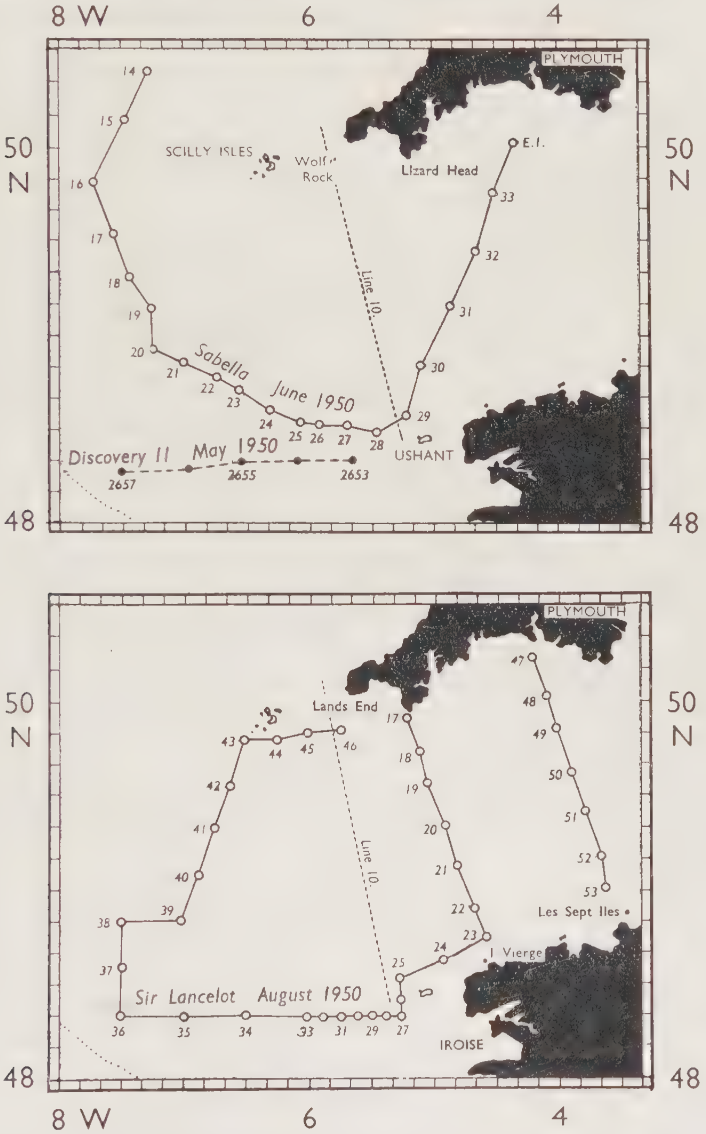
8 W
6
4
50 N
48
PLYMOUTH
SCILLY ISLES
Wolf Rock
Lizard Head
E.I.
Line 10.
Sabella June 1950
Discovery II May 1950
USHANT
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
2657
2655
2653
Lands End
Les Sept Iles
I Vierge
Sir Lancelot August 1950
IROISE
36
35
34
33
31
29
27
37
38
39
40
41
42
43
44
45
46
25
24
23
22
21
20
19
18
17
47
48
49
50
51
52
53

Fig. 3. Positions of observations in 1950 discussed in this paper. Upper diagram, 'Discovery' stations 2653–57 on 11 May and 'Sabella' stations 16–33 on 12–14 June. Lower diagram, 'Sir Lancelot' stations 17–53 on 6–13 August. Surface observations on line 10 are indicated.

The homogeneity of the August observations when plotted on temperature and salinity (T–S) diagrams was very good. Such few errors in salinity as there may have been were relatively gross (of the order ±0·1‰ salinity), suggesting leaky stoppers. Otherwise it would seem that the analyses, made in the Government Chemists' Laboratory, attained the highest precision of which the Knudsen technique is capable. On our own June cruise and on the other 'Sir Lancelot' cruises, precision may not have been so good.

Owing to the high quality of the August data and the very strong development of the thermocline some basic conclusions have been drawn and then applied to the earlier cruises. The last cruise will therefore be examined first but developed fully only for the region south of 49° 30′ N. lat. and west of 4° W. long. (Fig. 3). The line from Plymouth to Les Sept Iles had also been worked in July; the July records have been fully considered.

In the development which follows, a 'streamline' is a contour line within the sea along which waters with identical properties are found. The streamlines presented have been selected from along a gradient and are not confined to any plane surface. Some streamlines lie together like straws in a sheaf of corn, others may be curved not only in a horizontal plane, but in depth also.

Recognition of a streamline gives no indication of direction or intensity of current. Although several pieces of evidence combine to suggest that the movement of water west of Ushant in August is from south-west to north-east, for full confidence some current measurements are still needed.

To show the consistency of the observations, the argument of this section has to be detailed and intricate. Such presentation is necessary, first, because of apparent conflict with the well-argued papers by Dietrich (1950) and Hansen (1950), and secondly, as a worked example of how precision salinities such as the salinometer will produce in great numbers may be used when a strong thermocline is present. The general reader should obtain a sufficient understanding from Figs. 8, 9 and 12 alone.

The conflict with the German work is probably not real and is likely to be resolved by a detailed study of the distribution of mass and of wind, and of the thermodynamics of the south-western English Channel spread over 12 months.

The term 'water mass' is here employed in a very restricted sense.

The key stations were numbers 26 (20–40 m only), 24 (all depths) and 22 (all depths) on streamline *C* in Fig. 12 (p. 192). Temperature–salinity diagrams are displayed as Fig. 4A and vertical sections along the line of the streamline in Fig. 7, *C* (p. 186). The homogeneous water mass is there stippled and has a salinity of 35·35‰ within 0·01‰. These stations and streamline *C* firmly anchor to the land of the north-west corner of Ushant (Chaussée de Keleren or Keller) the system of streamlines to be developed.

The water at station 26, at 75 m and deeper (salinity 35·37–35·39‰, temperature 12·1°) was not moving east into the English Channel, neither was the water at 0 and 10 m depth where the salinity of 35·32‰ was not elsewhere recognized. Our interest rests on the water between 20 and 50 m with a salinity of 35·35‰ precisely and a range of temperature between 12·05 and 14·4° C. This water passed between station 25 and the Island of Ushant. Indeed there is no doubt that with the help of the strong tide it suffered considerable vertical mixing as it passed over the bottom in 38–50 fm. (70–90 m), between the steep-to submarine cliff of the Chaussée de Keleren and the off-lying submarine fosse to become the water mass observed at station 24. Here the salinity was unchanged and the range of temperature was reduced by mixing to 13·35–13·85° C at 10–90 m depth. All the water at station 24 proceeded unchanged to station 22 where it was found between 20 m and the bottom at 97 m.

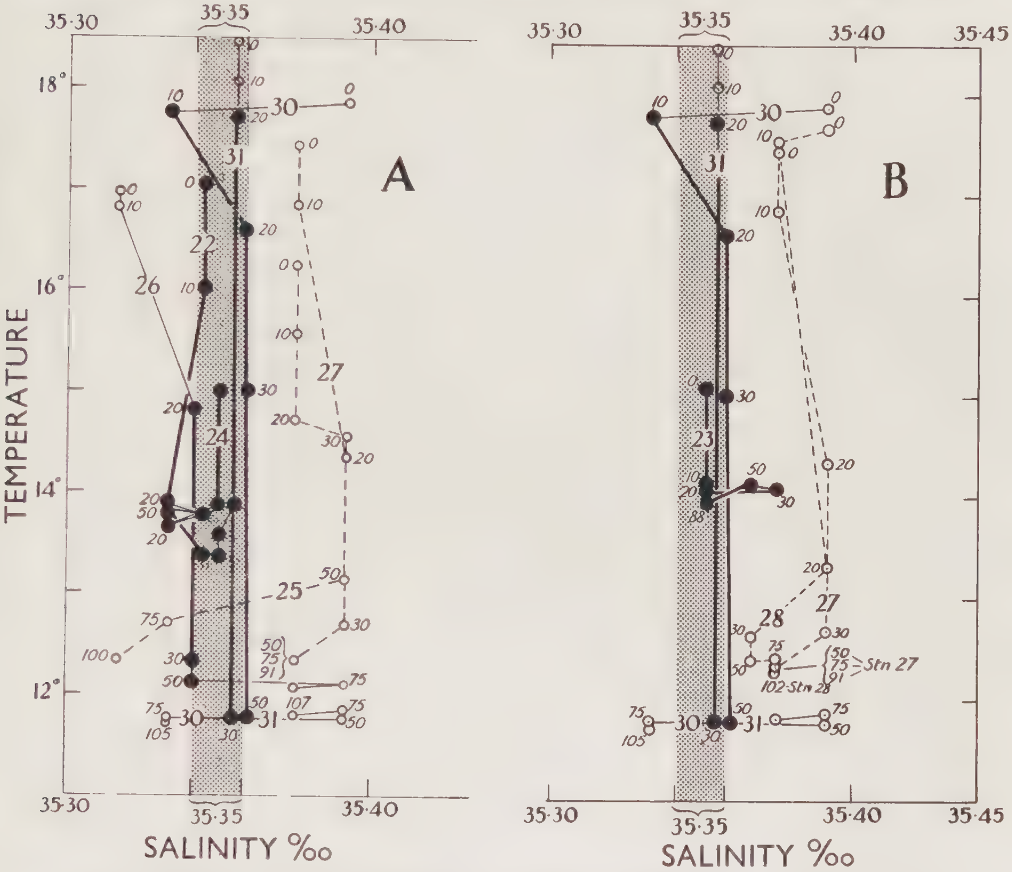

Fig. 4. Temperature–salinity diagrams from which the streamlines in Fig. 12 have been constructed: A, streamline *C*; B, streamline *B*. Cf. Figs. 7B, C and 9. To display the many points with salinity 35·35‰, the vertical line has been expanded into the shaded band.

The warmer water at station 22 (0–10 m) had been subjected to solar insolation. Its properties are compatible with a flow of water from station 30 (15–25 m deep) 15 miles west of Ushant.

On Fig. 4A, T–S curves (pecked) for stations 25 and 27 are included to show that the waters there were quite markedly different from that on the streamline *C* joining station 26 (20–50 m) to stations 24 and 22 (all depths).

The problem now is to find the previous travel of the water mass. It was not present immediately to the south at station 27 or at either of the adjacent stations 28 or 29; the water there at the appropriate depth was too saline. The T–S curve is fitted by that at station 30 down to 50 m and by station 31 down to 30 m (Fig. 4A). However, at stations 26 and 24 only water of this class colder than 15° C was present, the inference being that the thermocline level at stations 30 and 31 was making a disproportionate contribution to the north-easterly flow (Fig. 7, *C*).

Station 23 now needs special comment. Its T–S curve (Fig. 4B) carries an excrescence representing slightly more saline water than could have proceeded along the north-west shore of Ushant. There is no doubt that the excrescence represents a component of water (Figs. 7, 12, streamline *B*) from the area of stations 27 and 28 which had proceeded by way of the mile-wide Passage de Fromveur from the area of l'Iroise. This channel has a sill depth of about 40 m, accounting for the failure for deeper water from station 27 28 to reach the bottom (88 m) at station 23. Fig. 7*B* shows the continuity of properties over the sill of the Passage de Fromveur.

The water south and south-west of Ushant at stations 27, 28 and 29, more saline than that at 26, can have been moving only eastwards into l'Iroise and was not rounding Ushant north-about (Fig. 12, streamline *A*). This is the opposite of events in June.

Now we have to seek the origin of the water half-way across the Channel at station 20. At 0–30 m, it was very saline (Fig. 5A). The T–S curve accords with stations 29 and 33.

From station 29 it is impossible to find a course which may be reconciled with the observations at stations 25 and 26. From station 33 (between 30 and 45 m depth) the course (Fig. 12, streamline *E*) fits with the story that has still to be told.

Below 30 m at station 20 a different water mass was present. An origin from a position half way between stations 28 and 29 (not here illustrated) fits the T–S diagrams but is inconsistent with other stations or the pattern of geopotential anomalies. The vertical column at station 20 has therefore to be fitted by a surface sloping from a depth of about 28 m at station 32 (which sinks to the bottom at station 20) and 40 m at station 33 (which rises to 30 m at station 20). That is between stations 33/32 and 20, the T–S surface executed what an aviator would call a roll through more than a right-angle

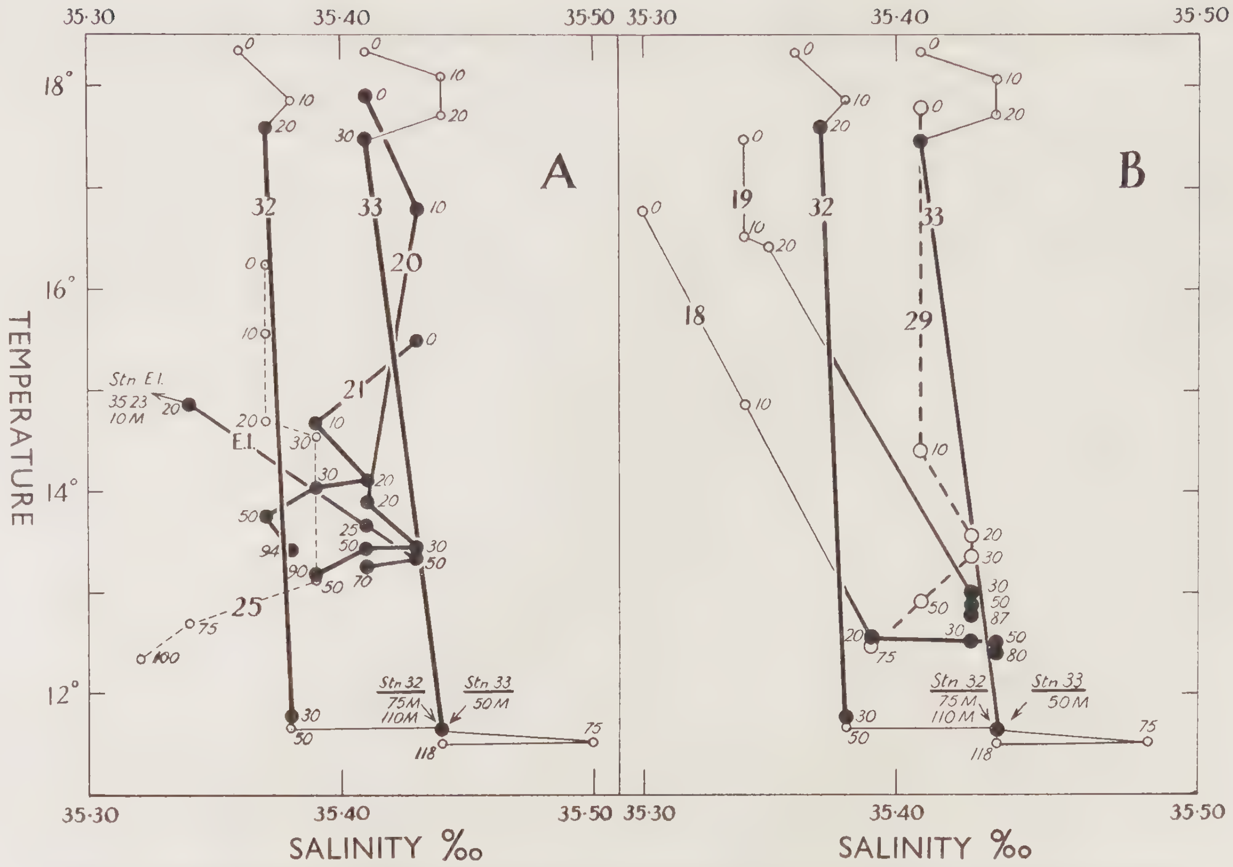

Fig. 5. Temperature–salinity diagrams from which the streamlines in Fig. 12 have been constructed: A, streamlines *D* and *E* (cf. Figs. 7D, 8, 9); B, streamline *F* as far as station 18 (cf. Figs. 7F, 9).

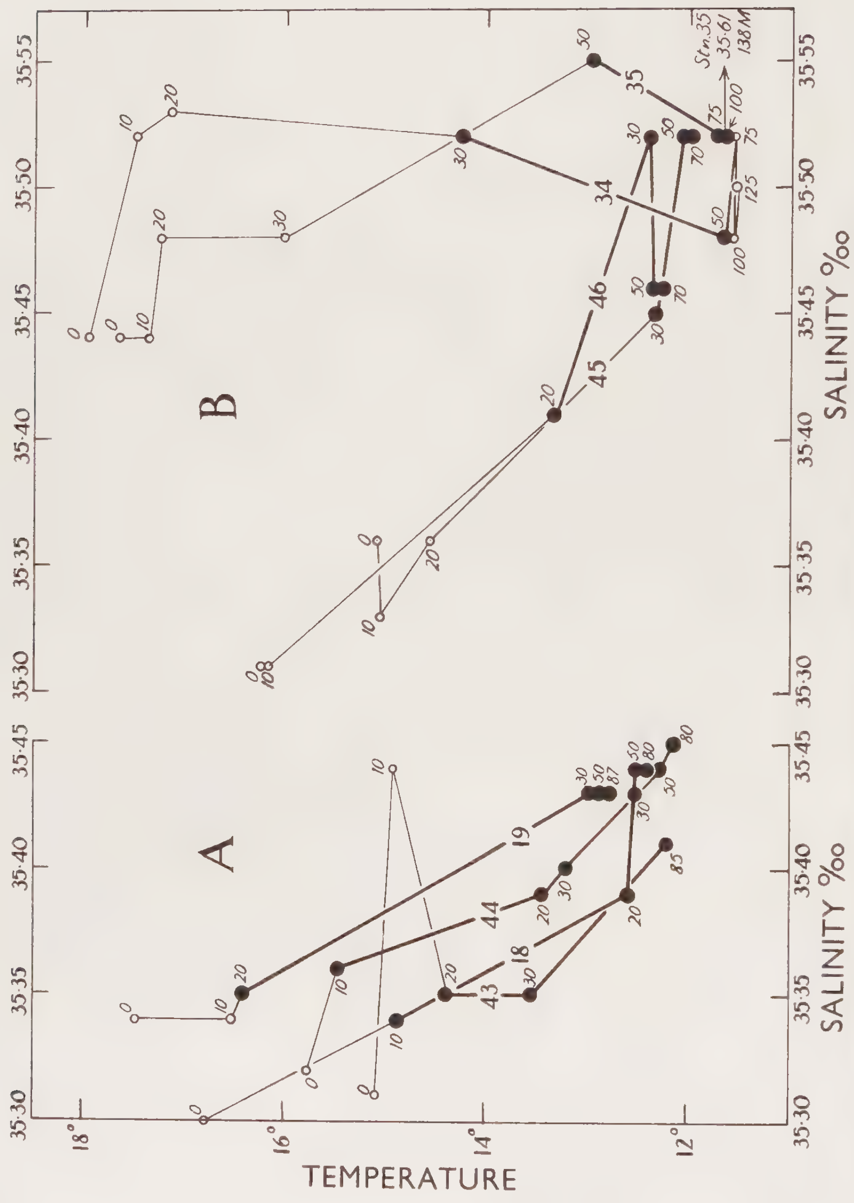

Fig. 6. Temperature–salinity diagrams from which the streamlines in Fig. 12 have been constructed. A, streamline *F*, north and north-west of station 19 (cf. Figs. 7F, 9); B, streamline *H* (not presented in section, but cf. Figs. 9, 12).

(Fig. 8). The direction of the roll was clockwise as the water advanced. In this deduction, temperature may legitimately be treated as a near-conservative quantity, since the water mass always remained subthermocline; Fig. 8 is necessarily somewhat schematic. It is not practicable to present this helical movement for every streamline though the tendency is present on all of them. Streamline *E* can be followed to 'Sula's' station E1 worked on 23 August (Figs. 5A, 8 and 12).

The water from station 32 (about 28 m depth), following streamline *E* in Fig. 12 passed station 25 at a depth of 50 m (Fig. 8) on its way to the bottom (90 m) at station 20, undercutting streamline *D*. Streamlines *D* and *E* at all points lay to the seaward of streamline *C* but north-west of Ushant by only a few miles.

Station 21 (Figs. 5A, 7) shows a similar history to station 20, but a larger proportion of the water came from the neighbourhood of station 32 and less from that of station 33. Moreover, the subthermocline water at station 21 was half a degree warmer than that at station 20 and consequently was somewhat higher within the thermocline at station 32.

A probable crossing-over between streamlines *D* and *E* represents water from station 32 which has passed station 25 at 50 m and then undercut somewhat shallower water on passage from midway between stations 32 and 33 at about 35 m north of station 25 to 21 (40–90 m). For clarity it has been eliminated from Fig. 12. It is not easy to represent the fanwise spreading and interlacing of these waters on plane diagrams.

Now let us consider (Figs. 5B, 7) stations 19 and 18, 24 and 14 miles S.S.E., respectively, of the Lizard. At this distance surface warming-up will have destroyed any hope of finding the history of the water above the thermocline but it would seem that temperature remained conservative below the thermocline. The very saline water (35·43–35·44‰ and temperature 12·47–12·92° C) between 30 m depth and the bottom at 82–87 m accords closely with the water in the lower part of the thermocline at station 33 (Figs. 5B and 12, streamline *F*, and the streamline *F* section in Fig. 7). Thus the water from station 33 was spreading fanwise, the upper thermocline water taking a more easterly direction than the deeper.

It would seem that 'Sir Lancelot' section between the Lizard and l'Ile Vierge, as between stations 20 and 18, lay almost along the line of movement of the current which had passed station 33 (48° 20′ N., 6° 00′ W.) at thermocline level.

This same water mass may be followed farther to station 44 south of Scilly (Fig. 12, streamline *F*, Fig. 6A, Fig. 7). Streamline *F* would seem to have passed north of stations 45 and 46, nearby the Wolf Rock. Still farther north another streamline (*G*) can be traced (Figs. 12, 6A) from station 18 (20 m, at the bottom of the thermocline there) to 43 (30 m to bottom in 85 m), i.e. along the south coast of Cornwall water which had crossed the Channel at the

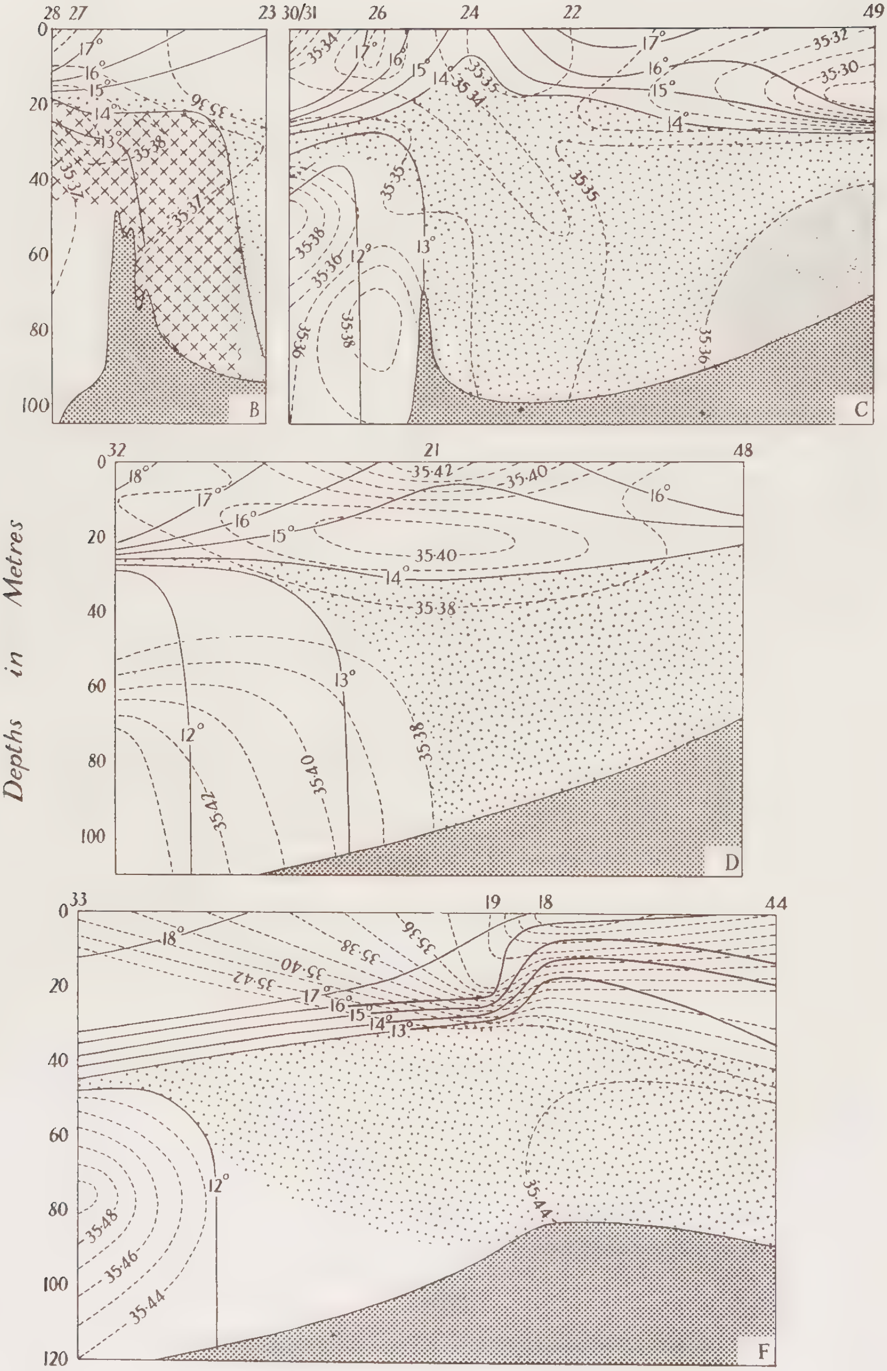

Fig. 7. For legend see opposite page.

bottom of the thermocline sank below a coastal belt of surface water to cover the submarine slope between 50 and 80 m depth.

The higher salinities at station 46 (30 m) and station 45 (49° 50′ N., south of the Land's End–Scilly Channel; at 50 and 70 m) are consistent with an origin in the lower part of the thermocline between stations 34 and 35 (48° 20′ N., 6° 45′ W., Parsons Bank area) (Fig. 12, streamline *H*, Fig. 6B).

The course of this concordant family of streamlines at the lower level is summarized in Fig. 12. They show that in the weeks preceding 6 August 1950, there had been a cyclonic circulation in the subthermocline water in the mouth of the English Channel and that most of this water had been introduced across the parallel 48° 20′ N., at thermocline level in a current there flowing east-north-east and grazing the north-west corner of Ushant. The destinations of the various parts of the thermocline structure along the parallel 48° 20′ N., are displayed in Fig. 9.

A spiral, the mirror image of the Ekman spiral, was evident west and north of Ushant, the water in the upper part of the thermocline along the parallel 48° 20′ N. proceeding to the right of that in the lower part of the thermocline there. Very little of the water truly below the thermocline moved into the English Channel. Such movement as it had was probably north-west.

So far we have examined the manner by which water which crosses the line west of Ushant within the thermocline fans out and deepens to become the subthermocline water on the line between the Lizard and l'Ile Vierge.

Legend to Fig. 7

Fig. 7. Sections along streamlines sublettered to correspond with Fig. 12.

Streamline B (area coarsely stippled) passes through the Passage de Fromveur between Ushant and the mainland of France (cf. T–S diagram, Fig. 4B). The water at 88 m at station 23 was identical with that at 8–9 m at station 24, i.e. at the top of the water in streamline *C* (next panel) which had sunk towards the east. Much of the cross-hatched water blanketing the slope of l'Ile Vierge inside of station 23 had unknown properties; to fit with the rest of this account it needed to have the properties of stations 27 and 28 between 20 and 50 m (T–S diagram, Fig. 4B, pecked lines).

Streamline C was anchored snugly to the north-west corner of Ushant (Chaussée de Keleren) (cf. T–S diagram, Fig. 4A). All but one of the points in the coarsely stippled area had a salinity precisely 35·35 ‰, so that only a generalized iso-line may be drawn for that salinity. The odd point was 35·34 ‰. The bottom water at station 49 was part of streamline *D*.

Streamline D (cf. T–S diagram, Fig. 5A, in part), lying to seaward of streamline *C*, is stippled. The elongated core of water at station 21 at between 12 and 28 m depth and having a salinity in excess of 35·39 ‰ had crossed the meridian 48° 20′ N. at 5° 56′ W. between stations 32 and 33 at a depth between 26 and 33 m. On Fig. 9, if inserted, it would show as a callosity on the left of streamline *D*. At station 21 it passed above section *D* and proceeded to station 51 as streamline *Q* (Fig. 10Q).

Streamline E cannot be presented as a vertical section. Its helical character is shown schematically in Fig. 8. It undercuts streamline *D* at station 25 at a depth of 50 m (cf. T–S diagram, Fig. 5A).

Streamline F (stippled) was established from a point 45 miles west of Brittany, across the mouth of the Channel, then south of Land's End and Scilly (cf. T–S diagrams, Figs. 5B, 6A).

The same process was at work in the thermocline on the Lizard–l'Ile Vierge line. Fig. 10 shows sections *P* and *Q* joining stations 22 and 52 and stations 21 and 51, where thermocline water is moving to the right of the water below the thermocline and sinking as it moves up-Channel. This is what might be expected of an anticlockwise gyral in the wide-mouth of a narrowing and shallowing channel in high summer.

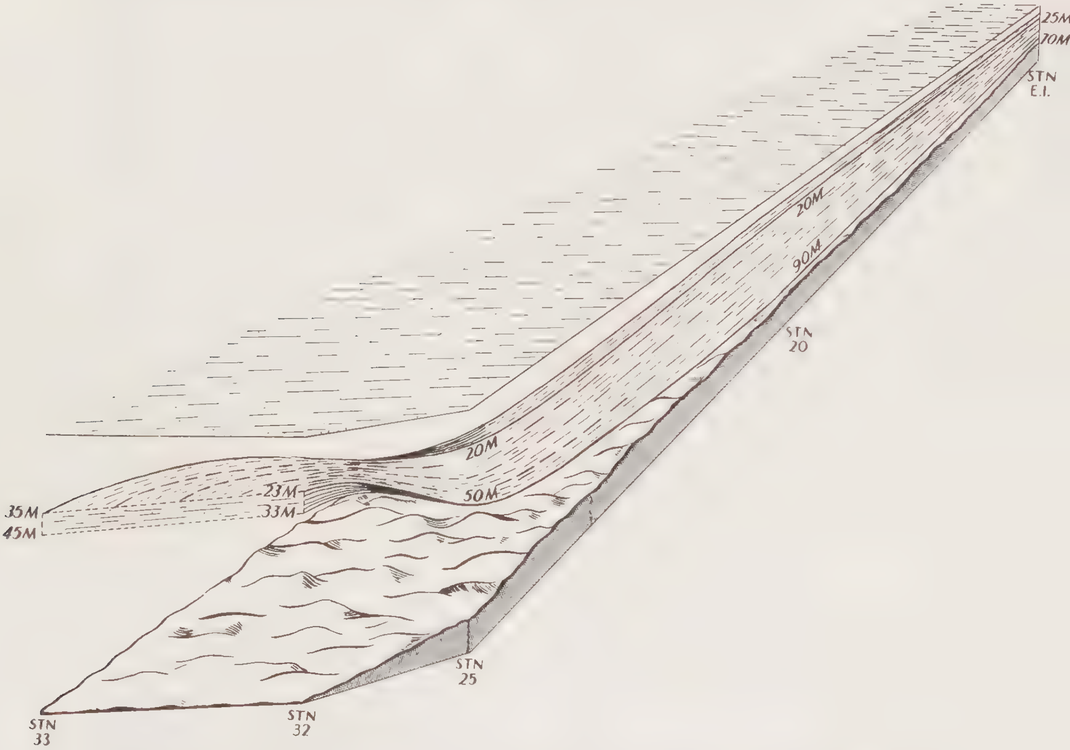

Fig. 8. A block diagram to show how water lying horizontally in the thermocline west of Ushant twists in a vertical plane through a right angle as it passes north-west of Ushant to occupy the subthermocline vertical column in mid-Channel (station 20) and at E 1. The lower contour passes through the position of station 25 at 50 m depth. The upper contour, however, passes not through station 25 but through a position some miles to the north-west. Some displacement of the isotherms and isohalines drawn in Fig. 7D is necessary but is compatible with the observations.

The course of these streamlines *P* and *Q* is also shown in Fig. 12. Streamlines *P*, *Q* and *G* lie above streamlines *C*, *D* and *F* where they cross.

The boundary between the easterly current (streamlines *P* and *Q*) and the deeper northerly or north-easterly current (streamlines *C*, *D* and *E*) was sharp. There is no evidence for water at the boundary depth at stations 20, 21 and 22 moving in an intermediate direction.

Consequently the thermocline 30 miles N.N.E. of Ushant was different

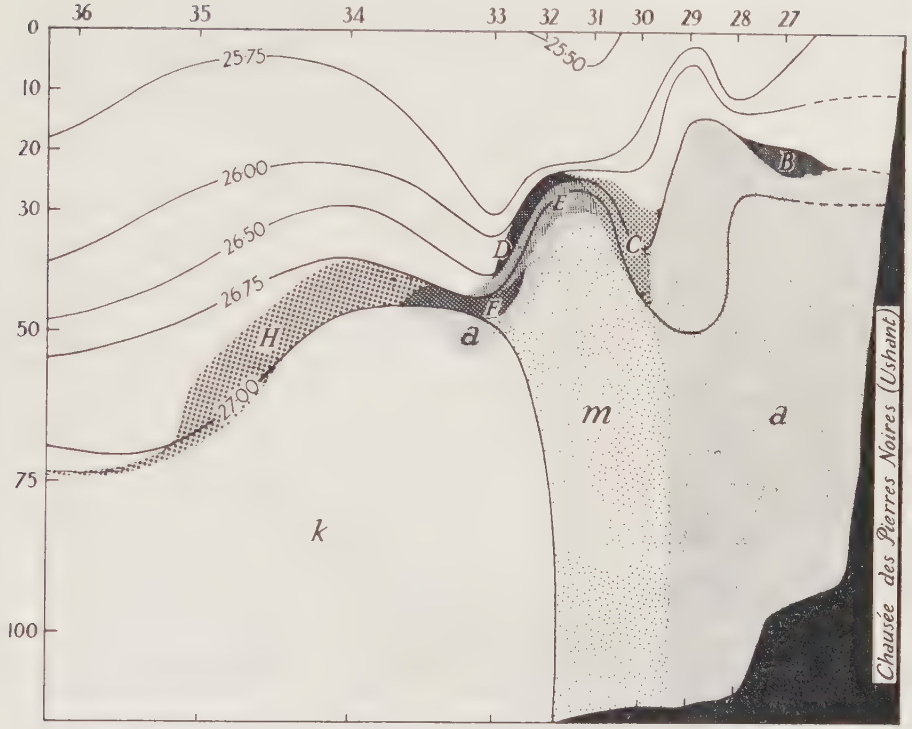

Fig. 9. Density (σ_t) section west of Ushant along lat. 48° 20′ N. on 7 August 1950 with destinations of the water in and below the thermocline. Waters which were to enter the English Channel east of a line drawn from Ushant to Scilly are denoted by capital letters, whereas lower case letters indicate waters which were not to enter the Channel.

Water masses *C*, *D*, *E* and *F*, subcomponents of one current system, were to flow along the corresponding streamlines (Fig. 12, also Figs. 4A, 5A, B, 6A) north-west of Ushant into the English Channel to occupy the whole water column between about 25 m and the bottom. Water mass *H* (Figs. 12, 6B) was to follow a similar course (streamline *H*) across the mouth of the Channel to a region south of the Wolf Rock.

The deep westerly water mass *k* was probably moving relatively slowly. Such movement as it had was towards the north. It never entered the English Channel.

Water mass *m* represents a vertical planar section of a spiral eddy. Near station 32 at about 45 m depth, the lowest water in the thermocline had a northerly spiral component. This flowed north-about station 31 and below water masses *F* to *C* to return as a slow current with a southerly component and occupying at station 30 all the water column below a depth of 50 m.

Similarly water mass *a* first lay in a vertical plane at 30–55 m between the water masses *F*–*D* which were to enter the English Channel and the water at the deep centre of the eddy (*m*). It also rotated, undercutting water mass *C* to become the deep water (below 20 m) in l'Iroise at stations 29, 28 and 27. The horizontal planar projection of the flow of water mass *a* is indicated on Fig. 12 as streamline *A*.

Apart from tidal movement water mass *a* in l'Iroise was probably almost stagnant in August. The small kernel of water marked *B*, to correspond with streamline *B* in Fig. 12, was really part of water mass *a* but in a position to be carried on the flood tide through the Passage de Fromveur to station 23 at 30–50 m depth (Fig. 4B).

Streamline *P* (Fig. 10) entered as a thin band of water immediately overlying water mass *C* in this figure; similarly the origin of streamline *Q* overlay streamline *D*. On this figure they are not easy to depict.

in structure and behaved differently from that 30 miles W.S.W. That to the N.N.E. was sharp between two layers moving in different directions; that to the W.S.W. was not a discontinuity but a transition layer 25 m thick in which a large amount of water was moving fast and undergoing helical partition. It is likely to provide a useful model of larger systems of the same kind.

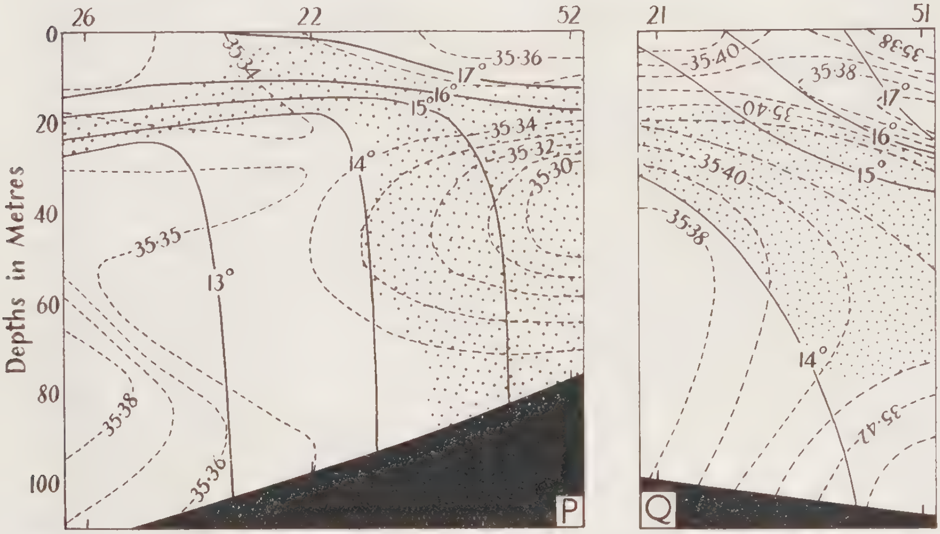

Fig. 10. Streamline *P* entered the Channel through station 26, immediately west of Ushant, between 19 and 27 m, then between station 25 and the island, to seaward of station 24 and then above the thermocline at station 22 where at depths between 3 and 19 m it crossed streamline *C*. It then sank to occupy station 52, 45 miles E.N.E., between 12 m and the bottom. Streamline *P* can be easily matched by interpolated values of temperature and salinity between stations 30 and 31 immediately above water mass *C* in Fig. 9.

Streamline *Q* also can be matched by interpolated values of temperature and salinity between stations 32 and 33 immediately above water mass *D* in Fig. 9. The elongated core of water with salinity 35·39–35·40‰ at 15–32 m depth around station 21 in Fig. 7C represents this water mass crossing over streamline *C* at an angle of intersection of +40°. It then passed up-Channel as shown here to occupy station 51 between 27 and 75 m depth.

The bottom water at station 51 gave an unsupported record of 14·29° C and 35·44‰. This is compatible with the water mass *a* which having flowed past station 33 at 50 m depth, ran north-about stations 32, 31 and 30 to proceed south-east into l'Iroise at station 29 (Fig. 9). However, no streamline can be constructed between any part of water mass *a* and station 51 without intersecting some other streamline. The result at the bottom at station 51 cannot be made to fit without unwarrantable complexity. It is more reasonable to ascribe it to an error of observation.

Two ways of presenting temperature and salinity at a depth of 50 m are shown in Fig. 11. The upper diagram shows a conventional chart where only the records from a depth of 50 m are considered and isotherms and isohalines in that plane are drawn by linear interpolation. It is grossly misleading. The lower diagram is drawn to conform with T–S diagrams, such as Figs. 4–6 and streamline drawings such as Figs. 7–9 and takes account of the changes in level of the water as it flows.

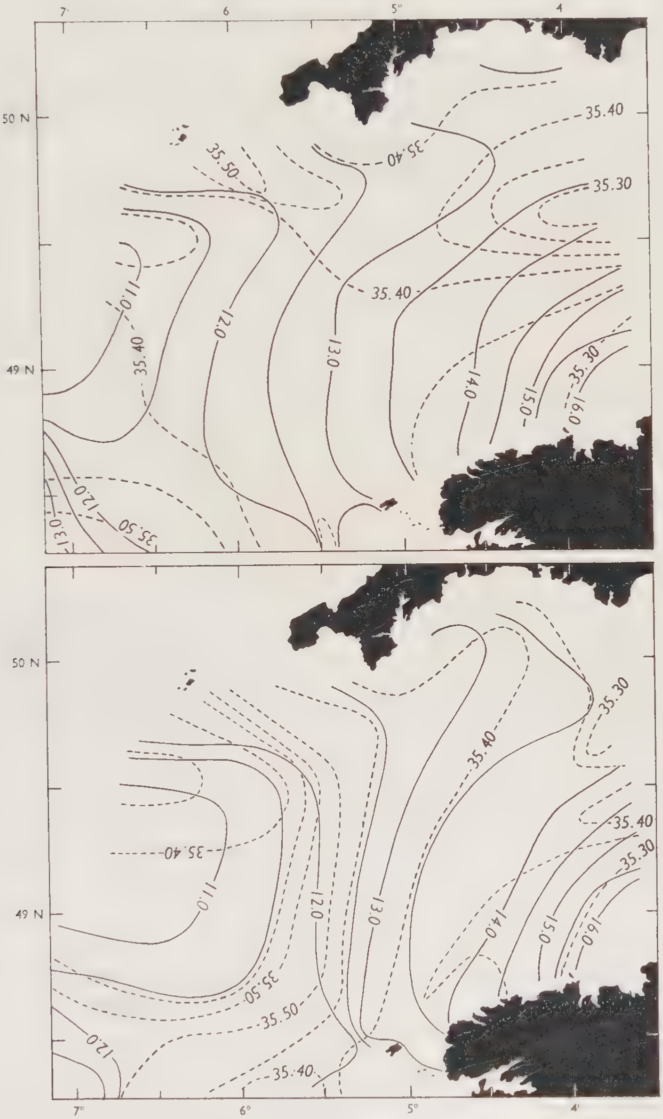
7°
6
5°
4
50 N
49 N
35.40
35.50
35.40
35.30
35.40
11.0
12.0
13.0
14.0
15.0
16.0
35.30
12.0
13.0
35.50
35.30
35.40
35.40
35.30
35.40
11.0
12.0
13.0
14.0
15.0
16.0
35.50
35.50
12.0
35.40
7°
6°
5°
4°

Fig. 11. Two ways of constructing isotherms and isohalines at 50 m depth from 'Sir Lancelot's' observation between 6 and 13 August 1950. The upper panel is drawn following standard conventions; the lower one is drawn to conform with the three-dimensional pattern of streamlines (see text). The position of the stations is shown in Fig. 3 (lower).

In shallow-water oceanography in summer, it would seem not merely interesting but essential to construct T–S diagrams for that part of the water column which is neither in immediate contact with the atmosphere nor subject to much absorption of radiant heat. It will be found that this approach not only forbids some interpretations which are otherwise attractive but gives much more confidence in the interpretations which remain. A comparison of Figs. 11 and 12 will show the close concordance between the streamlines, isohalines and isotherms for much of their course. Where they appear not to agree on a plane diagram, as west of Ushant and on streamlines *P* and *Q*, sinking is the cause.

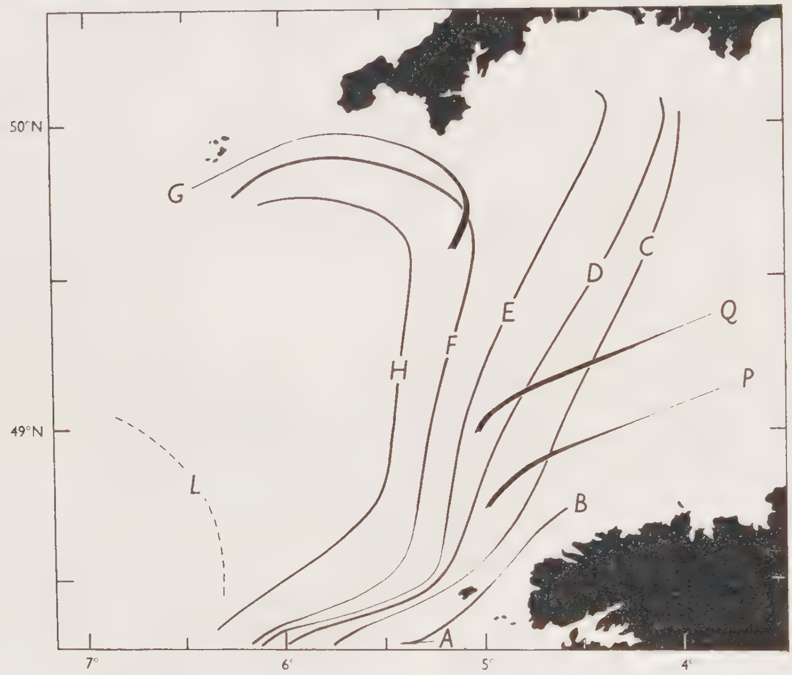

Fig. 12. The pattern of streamlines of the deeper water in August 1950. The direction of movement is from the south-west towards the north. Attenuation of the line indicates sinking, strengthening of the line indicates rising of a water stratum. To avoid confusion the southern courses of the streamlines *P* and *Q* past Ushant, where they are shallow and overlie the streamlines shown, are not drawn. The significance of streamline *L* is explained in the text and Fig. 17.

The T–S diagram technique cannot be surely applied to the upper waters subject to solar radiation and dilution by rivers. Even so the T–S diagrams and conventional charts of temperature and salinity at 10 m (not published) give no indication that there was any appreciable surface flow across the latitude 48° 20′ N. towards the English Channel. Most probably, as in May (to be discussed), it was towards the south-east.

It is remarkable that even in the upper layers some measure of conservation of properties is to be recognized. On the southern end of the line from Plymouth to Les Sept Iles at stations 50, 51 and 52 there is a surface stratum of water 20 m thick with temperatures exceeding 17° C and with salinities between 34·34‰ and 34·39‰. Very similar water was present on the Lizard–l'Ile Vierge line but only at the surface at stations 19 and 20 and nowhere else at any depth. The continuity of properties suggests a continuity of movement, i.e. that there was a thin surface current through stations 19 and 20 including water warmer than 17° C, and only a few metres thick, which fanned out to the east and south-east to become a warm surface stratum four times as thick. Moreover, the water having a temperature between 16 and 17° C at 5 to 15 or 20 m depth at stations 19 and 20, can also be followed but taking a somewhat more northerly direction.

This interpretation of surface water movements at high summer may be accepted only because it is compatible with the behaviour of the deeper streamlines.

The important conclusion is that there seems to have been a large recruitment of water into the mouth of the English Channel across the parallel 48° 20′ N. between 5° 35′ W. and 7° 00′ N. and this recruitment was from a layer at thermocline level about 20 m thick and forming part of a spiral the mirror image of that described by Ekman (1905) or, for tidal currents, by Hansen (1950).

Evidently, therefore, the spiral structure of the current is not controlled by wind but by the distribution of mass that comes into being when the summer sun shines on the Celtic Sea, on the water over the neighbouring continental slope and on the strongly tidal and shallow English, Bristol and Irish Channels.

Moreover, the recruitment of water to move into the English Channel, properly so-called, was confined between 5° 35′ and 6° 00′ W. long.

The whole argument requires and supports the hypothesis that when the change in density across the thermocline exceeds, say, one sigma-*t* unit, the temperature in the underlying water and in much of the thermocline itself may be treated as a conservative property.

The derivation from continuity of properties should be and is supported by the distribution of mass along the section 48° 20′ N. (Fig. 13). It is evident that the region between 'Sir Lancelot' stations 34 and 28 is one of strong currents or eddies, but, since there can be nothing approaching a surface of no motion and every surface slopes, it would be hazardous to deduce more than this from the geopotential topographies. They have, however, been most helpful in deciding that certain events were not possible.

This account of events associated with the month of August 1950 has had, for clarity, to be presented as though we then had an equilibrium state. Nothing is more certain than that we did not. Two points are at issue.

(*a*) We have traced streamlines between two or more points but the water in question had passed the first position some considerable time before it was observed at the later one. During this period of time the streamline may have writhed like a serpent in all three dimensions of space. Horizontal displacements may have amounted, and probably did, to many miles. Consequently at the time any water mass had crossed the parallel 48° 20′ N., its position may have been many miles from the position indicated in August. Streamlines have to be related to the sea water and not to the sea bed over which the water is passing.

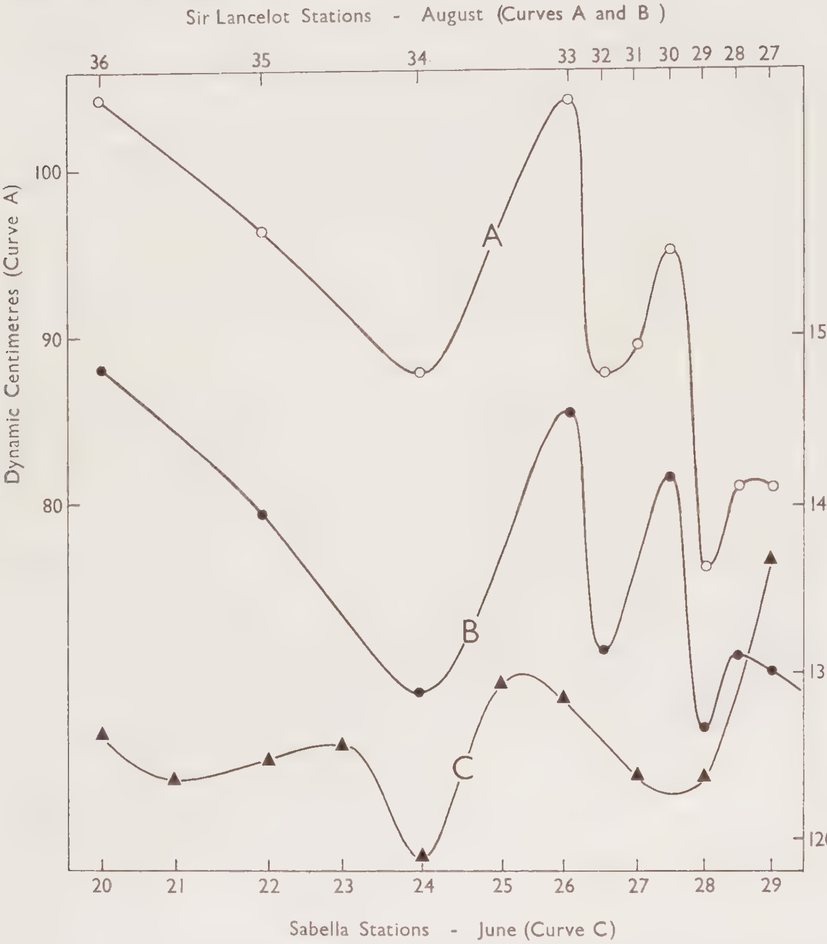

Fig. 13. Geopotential topographies: A, 'Sir Lancelot', 7 August 1950, along lat. 48° 20′ N., 0–50 db; B, the same, 0–100 db; C, 'Sabella', 13 June 1950, west of Ushant, 0–100 db. For station positions see Fig. 3.

(*b*) Smooth uniform flow at any depth in the sea seems to be rare. The bolus concept (Cooper, 1957) first developed for water cascading over a continental slope seems to be equally applicable to current systems over a continental shelf. Movement seems to proceed in surges, carrying boluses of water. Consequently the streamlines described must not be considered as bounding simple geometrical figures. When a surge of water passes, the streamlines bounding a water mass will expand to encompass a large body of water with similar properties. Between surges, the streamlines will close up, even to be nipped out altogether. Then very little of the characteristic water would be present.

In the past we have considered that the warming up during the summer of the deeper water at our station E 1 has been due to turbulent transport of heat vertically across the thermocline. This investigation suggests that this is an unnecessary hypothesis and that the rise in temperature after the thermocline is strongly developed is better explained by transport and sinking of water from the thermocline at and south of lat. 48° 20′ N. The origin of this thermocline, in its turn, now needs to be sought. Since this change of view has considerable biological significance, more work upon it would be wise before we accept it.

Density inversions in August 1950

At all 'Sir Lancelot' stations on 8 August 1950 between numbers 35 and 41 (except 35), there was an apparent density inversion around 75–100 m depth (Table 1) (cf. Spilhaus, Ehrlich & Miller, 1950). The apparent inversion

TABLE 1. DENSITY INVERSION IN SOUTHERN CELTIC SEA IN AUGUST 1950

(Minimum salinity and density in italics.)

	Station no. SL							
Depth (m)	33	34	36	37	38	39	40	41
	Temperature (°C)							
50	11·63	11·62	13·66	15·57	11·32	11·02	10·98	10·82
75	11·52	11·56	11·65	11·42	11·28	11·02	11·00	10·82
100	—	11·58	11·63	11·42	11·28	11·02	10·99	—
Bottom	11·51	11·58	11·62	11·42	11·28	11·01	—	10·82
	Salinity (‰)							
50	35·44	35·48	35·52	35·44	35·52	35·41	35·44	35·38
75	35·50	35·52	35·55	35·50	35·52	35·48	35·46	35·39
100	—	*35·48*	*35·53*	35·55	*35·46*	*35·44*	*35·44*	—
Bottom	*35·44*	35·50	35·55	*35·46*	35·52	*35·44*	—	*35·36*
Decrease in salinity	0·06	0·04	0·02	0·09	0·06	0·04	0·02	0·03
	Density (σ_t)							
50	27·02	27·05	26·68	26·20	27·14	27·11	27·14	27·12
75	27·09	27·09	27·10	27·10	27·15	27·16	27·15	27·13
100	—	*27·06*	*27·09*	27·14	*27·10*	*27·13*	*27·14*	—
Bottom	*27·04*	27·08	27·11	*27·07*	27·15	*27·13*	—	*27·11*
Decrease in density	0·05	0·03	0·01	0·07	0·05	0·03	0·01	0·02
Bottom sample (m)	118	125	148	140	130	125	100	110
Sounding (m)	124	133·5	155·	146	137	134	108	115

is due to changes in salinity rather than temperature. Although the variations in salinity are little greater than the titration error in Knudsen's method, the coherence of the data suggests that we must consider them seriously.

For a static system, the apparent inversion can be true only if we reject the principle of constant composition of sea salt. A dynamic explanation is more probable, namely, that the fast-moving water at thermocline level was associated with considerable water movement immediately beneath. This immediately subthermocline water had the properties of a projectile and so was able to maintain itself for some time above bottom water of slightly lower density.

The 'Discovery II' section in May 1950

The section over the slope between 48° 18′ N., 7° 30′ W. and 47° 24′ N., 7° 52′ W. has already been illustrated and discussed (Cooper, 1952, fig. 14). To quote: 'Assuming only horizontal water movements, the density gradient would indicate a weak east-bound current, flowing along the edge of the slope, in agreement with the current system already deduced for the region by Helland-Hansen and Nansen; but since vertical currents and internal waves may also have played a part no firm conclusions are possible. At least it seems that the impoverished warm saline surface water is more likely to have come from the ocean to the south-west than from the Biscayan shelf to the south-east.'

TABLE 2. EVIDENCE FOR CLOCKWISE BOTTOM CURRENT IN SOUTHERN CELTIC SEA, APRIL–MAY, 1950

Station ...	'Sabella' 16			—	'Discovery' 2654		
Date ...	19 April			19 April	11 May		
Lat. ...	49° 30′ N.			48° 20′ N.	48° 20′ N.		
Long. ...	8° 30′ W.			6° 06′ W.	6° 06′ W.		
Depth ...	140 m				124 m		
Depth sampled (m)	Temp. (°C)	Sal. (‰)	Inorg. P (μg-atom/l.)	Temp. computed by applying latitude correction	Temp. (°C)	Sal. (‰)	Silicate-Si (μg-atom/l.)
50	10·48	35·44	0·39	11·05	10·87	35·44	2·11
100	—	—	—	11·05	10·85	35·43	1·97
120	10·48	35·44	0·38	—	—	—	—

The most striking feature of the section on the shelf (Figs. 3, 14) along the parallel 48° 20′ N. in May was the cold core below 50 m at station 2654 (Table 2). The mean Celtic Sea latitude temperature for 48° 20′ N. (Cooper, 1960) for 3 weeks earlier was 11·05° C. There is no question but that this water was cold for the place and date. Intrusion as a submarine eagre from the south was impossible since the silicate content was only 2·0 μg-atom/l. This cold core can have come only from the north or north-west. The 'Sir Lancelot' sections across the English Channel on 8 April show that such high salinity water could not have come from there. In the 'Sabella' line on 19 April along the parallel 49° 30′ N. (Fig. 16), similar water is recognizable only at station 16 (Table 2).

The low phosphate at the bottom at 'Sabella' station 16 is also incompatible with an 'eagre' component, but the other properties suggest none the less that it must have approached station 16 from west-south-west or south-west.

The bottom configuration severely restricts the possibilities of what a bottom current may do. It is highly probable (Fig. 16) that the movement originated in an inflow over the indentation in the shelf at about 48° 50′ N., 9° 40′ W. (not as an eagre) and that its flow was controlled between the Cockburn, Jones and associated banks on the north-west and north and the Melville Knoll on the south. The Melville Knoll formed a fulcrum around which the current was compelled to turn. Its recognition at station 16 is so explained but, if the current had been streamlined, a greater influence might have been expected at station 15.

We have seen that horizontal currents, like cascading water masses, may tend to break up into writhing boluses. When such a current system is examined by a grid of stations it is a matter of chance whether one samples the core of a bolus or the envelope of water drawn in to fill the constriction between two boluses in sequence. If the bottom current shown in Fig. 16 is accepted, then it is necessary to accept as well the bolus hypothesis for horizontal currents.

The current would seem to have passed close to the position 49° N., 7° W., turning right under the influence of the earth's rotation. Its farther southward passage had then to lie east of Parsons Bank.

The first station on this section, no. 2653, lay 20 miles west of Ushant and could give no evidence as to whether any current was flowing close into Ushant. The surface observation from line 10 (Figs. 2, 3) on the following day at 48° 26′ N., 5° 16′ W., showed such a current at least weakly. The surface water had a density (σ_t) 26·84.

Combining the evidence from the distribution of salinity between 'Discovery' stations 2657 and 2659 and the evidence from the bottom water at station 2654, we have a picture of a current of saline water setting parallel with the break of slope, i.e. towards east-south-east. That none of this water was entering the English Channel in May is confirmed by the total absence of high salinity water (> 35·5‰) on 'Sabella's' June section a few miles farther north.

An application of this deduction may be to the spawning habits of the hake. The Melville Knoll, according to Hickling (1935), is one of its largest spawning centres. He believes that the success of the spawning depends on the prevailing winds setting the young fish towards the east into shallower water.

The probable set of the bottom current in 1950 suggests something rather different—a drift towards La Chapelle Bank where in June a rich and very characteristic euphausian type of plankton may occur in a narrow band parallel with the slope. The lead, slim though it is, seems worth further study.

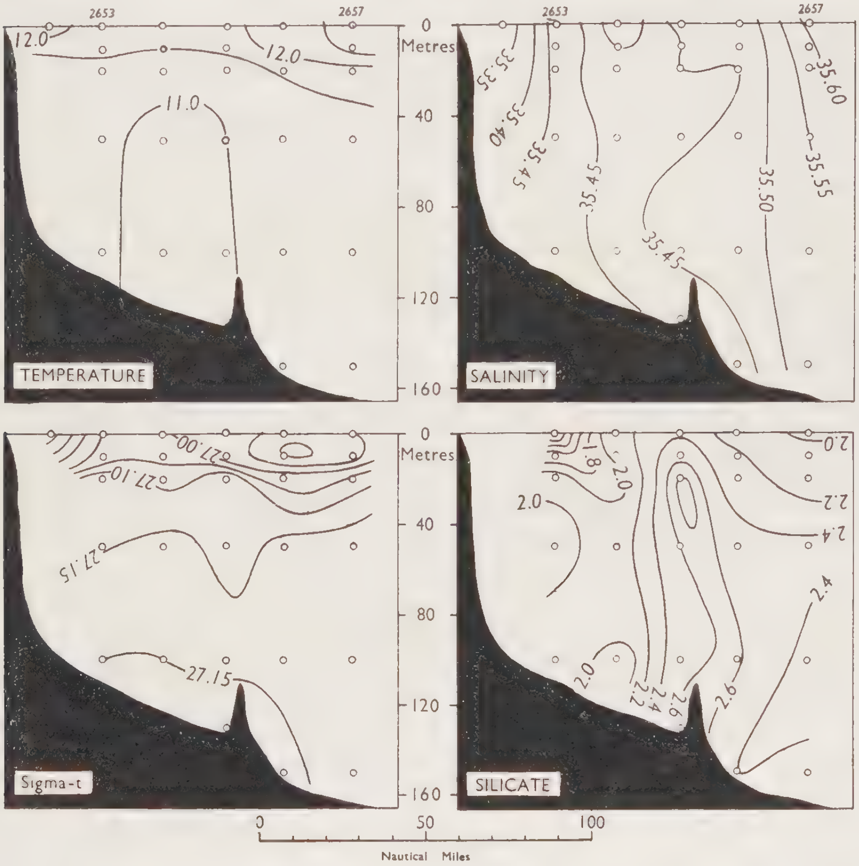

Fig. 14. Section along 48° 20′ N. lat. worked by R.R.S. 'Discovery II' on 11 May 1950; temperature, °C; salinity, ‰; density, σ_t; and silicate, µg-atom/l.

After the thermocline had developed strongly, water of the type found at 'Discovery' station 2655, but not necessarily from the position of that station, migrated north-westerly to be recognized at 'Sir Lancelot's' August station 40 (Fig. 17 and streamline *L* in Fig. 12).

The 'Sabella' section in June 1950

The course west of Ushant on 13 June 1950 is shown in Fig. 3 (p. 179), and the temperature, salinity and density in Fig. 15 (left-hand panels).

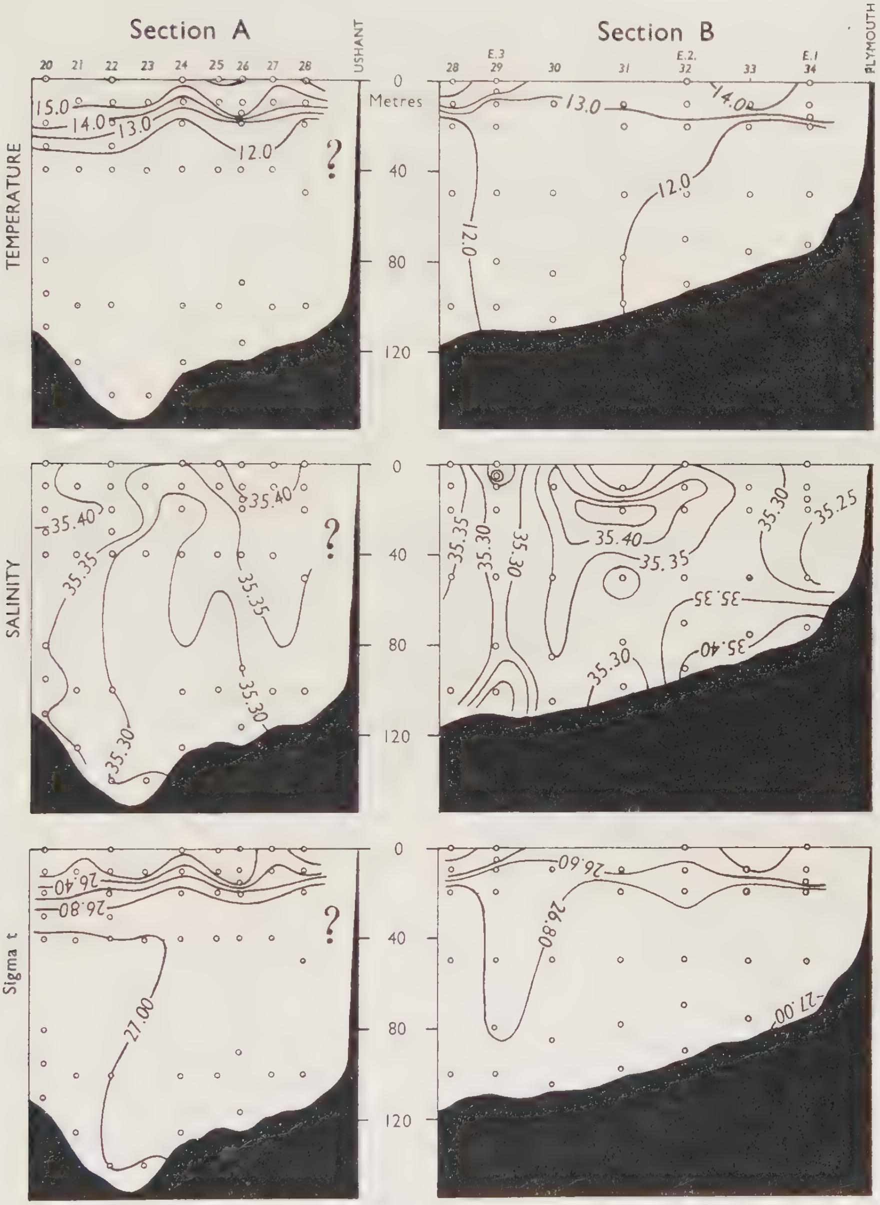

Fig. 15. Left-hand panels: 'Sabella' sections on 12–14 June west of Ushant (see Fig. 3) for temperature, salinity and density; station 29 probably represents the water between station 28 and the Island of Ushant. Right-hand panels for the line from station 28 through station 29 (E3) to Plymouth.

Except near Ushant the section is rather featureless. There is no evidence whatever of the high-salinity water observed by R.R.S. 'Discovery II' a few miles to the southward a month before. The water which was found by R.V. 'Sir Lancelot' in early August between the Lizard and l'Ile Vierge must have passed later on.

The thermocline had not developed sufficiently to warrant application of temperature-salinity diagrams as in August.

TABLE 3. PROPERTIES OF WATER AT 10 M AT SABELLA STATION 33 AND WEST OF USHANT

Station ...	29 = E3	33	28	27
Latitude N.	48° 34′	49° 45′	48° 29′	48° 31′
Longitude W.	5° 13′	4° 32′	5° 28′	5° 42′
Temperature (°C)	12·74	14·31	14·69	14·59
Salinity (‰)	35·26	35·34	35·38	35·44
σ_t	26·66	26·40	26·35	26·42
Total phosphorus (μg-atom/l.)	0·43	0·40	0·38	0·39

However, the water sampled (Fig. 15, right-hand panels) at station 29 (= E3, 48° 34′ N., 5° 13′ W., 7 miles N.W. by N. of Ushant) had properties quite different from the water at station 28 and the other stations to the south-west and west (Figs. 3, 15 and Table 3). Not only was the water more homogeneous with a temperature range of 1·8° instead of 4½° C, but no simple mixture, including the outside water as a component, could give the water found at E3. This was part of a coastal current which had been modified by turbulent passage over the Chaussée de Sein and the other off-lying reefs and islands along the west coast of Brittany and by admixture of fresh water from the Loire and other rivers. It had crossed the section shown in the left-hand panels between station 28 and Ushant and is denoted by an interrogation mark.

Though the water at E3 (station 29) had little in common with that to the west (stations 28, 27, etc., in Figs. 3, 15), that to the north (stations 30 and 31, Fig. 15) had much in common. The one had contributed to the other.

Since the bottom of the thermocline occurred at about 40 m (~40 db) and samples were drawn from this depth at nearly all stations, it has been used for drawing charts of relative geopotential topography (Table 4, cf. Fig. 13) over the whole area. That for 40 against 100 db shows a strong relative current flowing close to Ushant from the Biscayan coast of Brittany into the English Channel. Both by the Bjerknes circulation theorem (Sverdrup, Johnson & Fleming, 1942) and by Harvey's (1929) simple derivation, the current at 40 m was not less than 4 miles per day.

There is little doubt that this represents a northward moving coastal mid-water current, strongest at 40 m, and not a reverse current strongest at the bottom. The chart for the current at the surface relative to that at 40 m indicates either a surface current towards the south or a current at 40 m towards the north. Here, to reconcile the two charts, the second explanation must be true.

Dissection of geopotential anomalies at stations 29 to 26 (Table 4) shows that the components of relative current were small within the 20–40 m layer and were largely confined to the layers above 20 m and below 40 m, as required by the theory. The maximum strength of the north-flowing current therefore lay somewhere in the 20–40 m stratum.

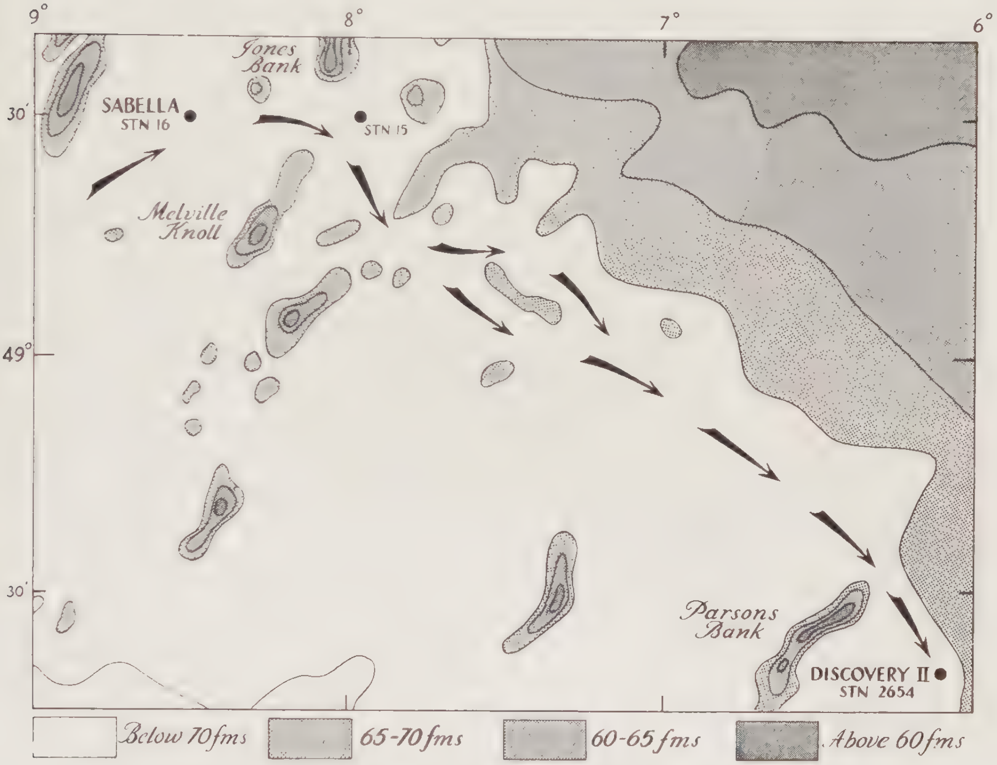

Fig. 16. Probable course of a bottom current in April–May 1950.

Much of the water entering the English Channel at the time had temperature between 12·3 and 12·5° C, salinity about 35·3‰, density (σ_t) about 26·7–26·8, total phosphorus 0·45 μg-atom/l. This warm, nutrient-poor bottom water was found north of Ushant for more than 30 miles. The situation was closely similar to that found north of west Cornwall.

The inflexion in geopotential farther west at station 24 in all curves involving the surface was not shown in the curve for 40 against 100 db. It was due to a shallow (0–20 m depth) current of cold, relatively low-salinity water, but whether this was an eddy from the Ushant corner current or whether it came from the north cannot be decided.

This picture is relative. The whole of the water as far west as 7° 45′ W. was moving slowly northward, a movement which needs to be superimposed upon the relative corner currents at Ushant.

TABLE 4. ANOMALIES OF GEOPOTENTIAL WEST OF USHANT, JUNE 1950, DYNAMIC CENTIMETRES

Depths compared (m)	West	Station		East
	26	27	28	29
0–20	3·67	—	3·25	3·00
20–40	2·45	—	2·33	2·65
0–40	6·12	5·73	5·58	5·65
40–100	6·71	6·66	6·38	7·98

TABLE 5. DENSITY INVERSION NEAR USHANT IN JUNE 1950

(Minimum salinity and density in italics.)

	Station no., 'Sabella'				
Depth (m)	31	29	28	27	26
			Temperature (°C)		
40	—	—	—	11·59	11·56
50	12·13	12·39	11·59	—	—
78–80	12·00	12·33	—	—	—
90	—	—	—	—	11·51
98–100	12·00	12·36	11·59	11·58	—
116	—	—	—	—	11·55
			Salinity (‰)		
40	—	—	—	35·41	35·37
50	35·29	35·29	35·35	—	—
78–80	35·32	35·30	—	—	—
90	—	—	—	—	35·30
98–100	*35·26*	*35·19*	*35·34*	*35·34*	—
116	—	—	—	—	*35·28*
			Density σ_t		
40	—	—	—	27·00	26·98
50	26·80	26·75	26·96	—	—
78–80	26·85	26·77	—	—	—
90	—	—	—	—	26·93
98–100	*26·81*	*26·68*	*26·95*	*26·95*	—
116	—	—	—	—	*26·91*
Sounding	103	110	115	119	124

No water from westward of the meridian 5° 30′ W., and below 30 m in depth had entered the English Channel. There is some evidence that a little of the surface water of the kind found in the water westward of Ushant (stations 28–26) had reached station 33 (Figs. 3, 15) (Lizard Point 29 miles 209°) on the English side of the Channel. Apart from this no water from west of 5° 30′ W. crossed the Plymouth–Ushant line, a situation very different from that found in August.

In August we had evidence for a density inversion beneath the water moving fastest, so also have we in June (Table 5). On this occasion the fast-moving water and apparent density inversions were both grouped around Ushant. A similar explanation, no doubt, applies.

The sequence of events in the summer of 1950

The prevailing winds of this sea area are from the south-west and west. Such winds will tend to initiate surface currents towards the east and south-east. Wind-induced currents, at greater depths will tend, according to the theory of the Ekman spiral, to set still farther to the south.

Under these conditions there will be no tendency for the wind to set homogeneous water from south of 48° 20′ N. into the English Channel. This agrees with the findings by R.R.S. 'Discovery II' in May.

The same prevailing winds will tend to initiate the same kind of currents in homogeneous water at any time of year, whatever the water temperature, so that these winds should never set water from west of Ushant into the English Channel (cf. Cooper, 1960). Under these conditions recruitment of water into the Channel from the west should be from north of 49° N. lat.

As soon as the thermocline begins to form, the wind will cease to influence the direction of movement of the deeper water. This will tend to move solely in accordance with the distribution of mass over the whole of the Celtic Sea, its bounding continental slope and the English, Bristol and Irish Channels.

As an empirical finding we can say that as the summer advanced the direction of movement of the deeper water in 1950 changed. The north-easterly movement first appeared in June as a coastal current around Ushant from the west coast to the north coast of Brittany.

As the thermocline strengthened, the site of the current entering the English Channel moved westwards. Water bound towards the English Channel was then confined to a thermocline layer about 20 m thick and crossing the parallel of latitude 48° 20′ N. between 5° 35′ W. and 7° 00′ W. That part bound for the English Channel east of the Lizard headland was restricted to the range of longitude 5° 35′–6° 00′ W. This current impinged on the north-western corner of Ushant.

At any time of year, heavy rainfall over western France and consequent river outflow to the sea will lead to a strong coastal current around Ushant. This will over-ride or supplement the circulation arising from the heat balance in the water to the westward and northward.

This reconstruction needs confirmation. It will be difficult to extract from our earlier records since our standard stations are too far apart. It would not have been possible to deduce this account if we had had data only from 'Sir Lancelot' August stations no. 25 and 34 and from 'Sabella' June stations 29 and 23, equivalent to international stations E3 and E4.

The influence of these events on the English Channel as a whole and comparison with other years (Matthews, Lumby and Harvey) will be deferred. Preliminary comparison with the work of Dietrich (1950) has already been made. Further comparison is best achieved not by argument here but by seeking more measurements.

A comparison with the distribution of biological indicators is also deferred but mention may be made of the close parallel with Russell's (1935) findings. In his fig. 4 he sets out the arrival of south-western water off Plymouth in mid-August, 1930, 1931, 1932, in July 1933 and September 1934.

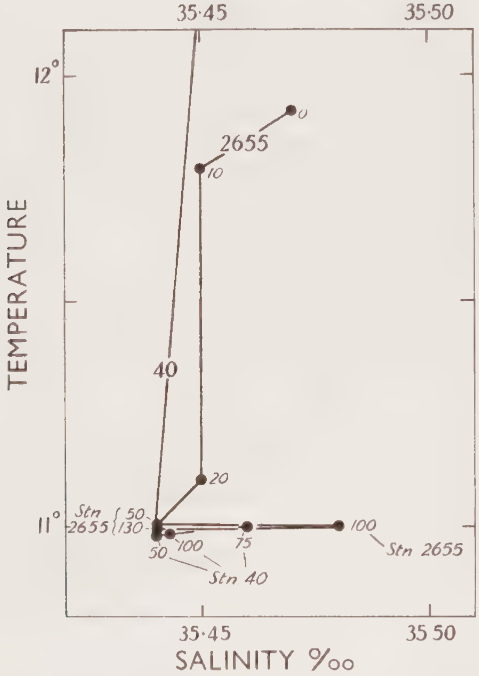

Fig. 17. Temperature–salinity diagrams for the water at 'Discovery' station 2655 (48° 20′ N., 6° 34′ W. on 11 May) and 'Sir Lancelot' station 40 (49° 02′ N., 6° 52′ W. on 8 August 1950); streamline *L*. To conform with the other streamlines transport to the north must have occurred mostly in the month before the August observation.

THE PARTITION OF PHOSPHATE

For many years in the English Channel near Plymouth inorganic phosphate at the winter maximum has averaged about 0·45 μg-atom/l., three-quarters of that available in the Bay of Biscay from which by a more or less direct route the water of the English Channel is recruited. It has long been a problem as to how 0·15 μg-atom/l. of inorganic phosphate or so is permanently removed from the water.

The present study provides the answer for about half of this. In 1950 we hoped that total phosphorus would prove a more nearly conservative property than inorganic phosphate; it also has the advantage of not requiring analyses to be made at sea. It has not proved conservative, so that analysis of total phosphorus has lost favour. Samples from 10, 20 and 50 m and greater depths were sampled by R.V. 'Sir Lancelot' on the cruise of August 1950 and analysed at the Plymouth Laboratory by Harvey's methods by Mr F. A. J. Armstrong.

Due to the problems of particulate distribution of phosphorus in living organisms and in detritus (seston) (cf. Cooper, 1948, for the parallel problem with iron), analyses of total phosphorus are less reproducible than those of inorganic phosphate. None the less, the August 1950 analyses are sufficiently precise to make my point.

First, let us consider all the analyses of total phosphorus at stations 30–34 between which at thermocline level water was entering the western English Channel. The mean of the eighteen analyses of bottom water below the thermocline is at 11·67 ± (S.D.) 0·09° C and 0·62 ± (S.D.) 0·04 μg-atom/l. of total phosphorus. This is taken as a measure of the winter stock of total phosphorus available to enter the Channel. It may be somewhat lower than the average.

There is another cluster of nine analyses on the warm upper water with mean at 17·75 ± (S.D.) 0·20° C and 0·305 ± 0·02 μg-atom/l. total phosphorus. The straight line which joins the two centres of gravity leaves three analyses within the thermocline about 0·02 μg-atom/l. to the right.

This straight line has been used to estimate what the total phosphorus content in the deeper water at stations 25–18 and 45–43 should have been if it had suffered no change during passage from the thermocline at latitude 48° 20′ N. to the observed position (Table 6, col. 3). In the next column (col. 4) is given the content of total phosphorus observed. Column 5, representing the loss by thermocline partition, is the difference between 0·62 μg-atom/l. and the computed value in col. 3.

At the stations near Ushant (25–23) where the time of travel was short and there was no opportunity for further partition, the computed and observed values agree well. The loss unaccounted for is small. As, however, we go northward and the travel time of the water becomes greater, the loss in total phosphorus unaccounted for becomes greater. A calculation in terms of density instead of temperature gives a similar result.

The physical partition occurring at the thermocline at 48° 20′ N. therefore accounts for about one-half of the loss regularly observed off Plymouth. The fate of the other half will be considered when the physical and chemical oceanography of the English Channel in 1950 comes to be published.

TABLE 6. LOSS OF TOTAL PHOSPHORUS ON PASSAGE BETWEEN THE BAY OF BISCAY AND THE WESTERN ENGLISH CHANNEL

		Total phosphorus (μg-atom/l.)			
				Loss of ΣP	
Station, 'Sir Lancelot'	Depth (m)	Computed graphically	Observed	By thermocline partition	Unaccounted for
25	50	0·55	0·53	0·07	0·02
	75	0·57	0·54	0·05	0·03
	100	0·59	0·56	0·03	0·03
24	50	0·52	0·57	0·10	−0·05
	90	0·53	0·53	0·09	Nil
23	50	0·49	0·47	0·13	0·02
	88	0·50	0·50	0·12	Nil
22	50	0·51	0·46	0·11	0·05
	92	0·53	0·51	0·09	0·02
21	50	0·51	0·46	0·11	0·05
	94	0·53	0·50	0·09	0·03
20	50	0·53	0·46	0·09	0·07
	87	0·54	0·50	0·08	0·04
19	50	0·56	0·43	0·06	0·13
	80	0·56	0·47	0·06	0·09
18	50	0·58	0·48	0·04	0·10
	73	0·58	0·49	0·04	0·09
46	—	—	No analyses	—	—
45	50	0·60	0·52	0·02	0·08
	70	0·60	0·54	0·02	0·06
44	50	0·59	0·49	0·03	0·10
	80	0·60	0·54	0·02	0·06
43	85	0·59	0·52	0·03	0·07

ON PRESENTATION

This paper has been difficult to write and may prove even more difficult to read. None the less it is a foretaste of what may come apace when the increasing application of the salinometer makes it possible to unravel certain movements of stratified waters in great detail. Biologists need such information but, confronted with it, may recoil in horror. Physical oceanographers may therefore need to consider how they can systematize the extraction and presentation of the desired information. Probably diagrams, such as Figs. 4–7 presented here solely to illustrate a worked example, should be pigeon-holed when they have served their turn and publication restricted to diagrams such as Figs. 9 and 12 and the minimum of textual description. It may be necessary to develop a block diagram form of presentation on the lines of Fig. 8. The possibility of criticism should have vanished so that conclusions would need to be taken on trust. Comment will be appreciated.

The author is greatly indebted to Mr G. A. W. Battin for his excellent illustrations. Without these the paper would have been even more turgid.

He is also grateful to Lt.-Cdr. C. A. Hoodless, D.S.C., R.N.R., then master of R.V. 'Sabella', and his crew for much help in 1950; also to Mr David Vaux of the Lowestoft Laboratory for making data and diagrams of 'Sir Lancelot's' cruises quickly available.

SUMMARY

The currents around a prominent headland, the island of Ushant between the Bay of Biscay and the English Channel, are discussed.

The flow in the spring of 1928 has been re-examined. Run off from the Loire watershed reached Ushant in March. North of Ushant it spread out before passing up the English Channel on the French side. Some of this water spread northwards from Guernsey towards England and reached the neighbourhood of Plymouth by mid-April and the Seven Stones Light Vessel a fortnight later, i.e. the flow was cyclonic within the western bight of the Channel and took about 10 weeks to travel from Ushant to Land's End at a rate over the ground of 3 miles a day.

In May 1950 currents in the southern Celtic Sea were setting east-south-east parallel with the slope. No water there was moving towards the English Channel in May and June. The bearing of this result on successful hake spawning is briefly discussed.

In June 1950 a narrow coastal current, strongest at about 40 m depth, was setting round Ushant and fanning out in the English Channel north of Brittany; however, no water from west of 5° 30′ W. long. was then entering the Channel near Ushant.

Once the thermocline had become well established the pattern of currents changed completely, as shown by closely spaced stations worked by R.V. 'Sir Lancelot' in August. The salinities have the greatest precision attainable by the Knudsen technique and have made possible a detailed study of current streamlines. It is assumed that properties beneath the thermocline were conservative. Using temperature–salinity diagrams, a sheaf of streamlines has been constructed which, except for 1 salinity out of about 120 which are relevant, form a completely coherent pattern. There was a large recruitment of water into the mouth of the English Channel across the parallel 48° 20′ N. between 5° 35′ W. and 7° 00′ W., and this recruitment was from a layer at thermocline level about 20 m thick. The deeper water followed the streamlines, *A–F* and *H* in Fig. 12. These thermocline waters were undergoing a partition, the shallower waters setting to the right of the deeper and sinking while so doing (streamlines *G*, *P* and *Q*). This mechanism explains in part the excessive warming up of the south-western English Channel to which Dietrich drew attention. There is an apparent conflict with some of the German conclusions which will need further sea work to resolve.

This mechanism accounts for about one-half of the impoverishment in

phosphate observed as between the Bay of Biscay and the winter maximum in the English Channel.

Slight density inversions occurred in June and August.

In order that the conclusions may be fairly criticized much intricate scaffolding has had to be presented. This may have obscured the results of interest to biologists.

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MASSIVE UPWARD DISPLACEMENT IN THE DEEP OCEAN

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(Text-figs. 1 and 2)

For a third of a century many and varied studies on sea water have been concentrated upon a single accessible shallow-water station in the English Channel, E1, supplemented by more extensive excursions usually designed to test working hypotheses. This concentration of effort has been richly rewarded. In deep-water oceanography a similar approach is appropriate; a standard station, 'Cavall' has therefore been selected in the north-eastern Bay of Biscay in 4700 m of water at lat. 46° 30′ N., long. 8° 00′ W., nominal, a position worked by the Danish Research Vessel 'Dana' in 1922 and 1930. It is not only the nearest deep water position to Plymouth but it has best possible coverage by the Decca Navigator system. For our experimental programme it is essential that the station positions be maintained and repeated precisely. To achieve this a working Decca chartlet (Fig. 1) on a scale of 1:20,000 has been prepared for each station from a portion of the Admiralty Decca Lattice chart no. L 1104. On this a circle of radius one mile is inscribed. Throughout operations the ship is maintained within this circle by stopping work when necessary and steaming back on Decca co-ordinates towards the centre, or beyond to pre-compensate expected drift.

On a number of occasions the deep-water station Cavall has been fixed astronomically. The position found is 6 km from the nominal. The discrepancy may arise from error in the 50-fold expansion of the small scale chart or from distortion of the Decca Lattice over the sea area. It is of no practical consequence so that, although a correction could now be made, to do so would lead only to confusion. In station lists and precision statements the astronomical fix, 46° 27′ N., 8° 02′ W., will need to be reported but in descriptive statements the easily remembered nominal position will continue to be used. In both cases the over-riding definition is by Decca co-ordinates: Red G 21.55, Green D 44.90, which alone matter for navigation.

Two more standard stations (Table 1) have been established on course from Plymouth over the continental slope of La Chapelle Bank and one precisely at the break of slope which is very sharp (Cartwright, 1959, Fig. 2, upper). A further shallow water station over the Bank is sometimes worked 9 miles within the break of slope.

It has become essential to have convenient names for these stations and I have selected some from Celtic mythology.

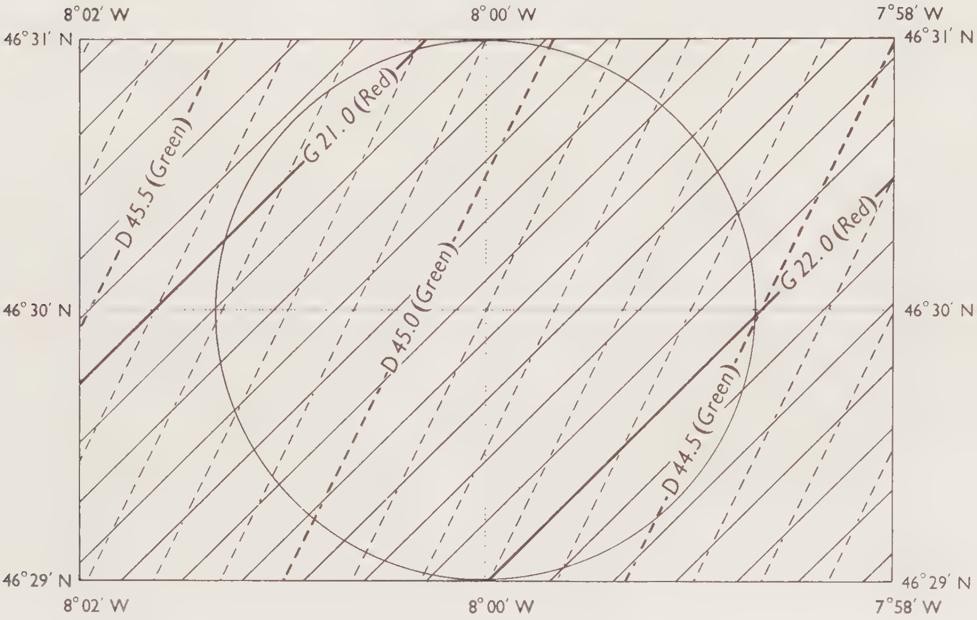

Fig. 1. Working chartlet (scaled 1:20,000) used for maintaining station Cavall within a circle of radius 1 mile using the Decca Navigator system.

TABLE 1. POSITION OF STANDARD STATIONS, BAY OF BISCAY AND LA CHAPELLE BANK

Station	Nominal position		Astronomical position		Decca Co-ordinates		Depth (m)
	Lat. N.	Long. W.	Lat. N.	Long. W.	Red	Green	
Geraint	47° 45′	7° 05′	Not known		F 22.20	D 45.00	—
Ysolde	47° 35′	7° 12′	Not known		G 02.50	D 44.60	175–185
Arthur	47° 30′	7° 18′	Not known		G 03.69	D 45.57	Variable 800–1400
Bedivere	47° 20′	7° 22′	Not known		G 08.46	D 44.28	Variable 3100–3800
Cavall	46° 30′	8° 00′	46° 27′	8° 02′	G 21.55	D 44.90	4710

UPWARD DISPLACEMENT

Views already published (Cooper, 1955*a*, *b*, 1956; cf. Dietrich, 1956) require that room for the water sinking into the eastern North Atlantic from the Iceland–Faroe Ridge may be found only by upward displacement somewhere or other of water already there. In any one year it was envisaged that this effect would not exceed 7–10 m and that northern water was most unlikely to intrude at the very bottom of the ocean. The 1956 programme was designed

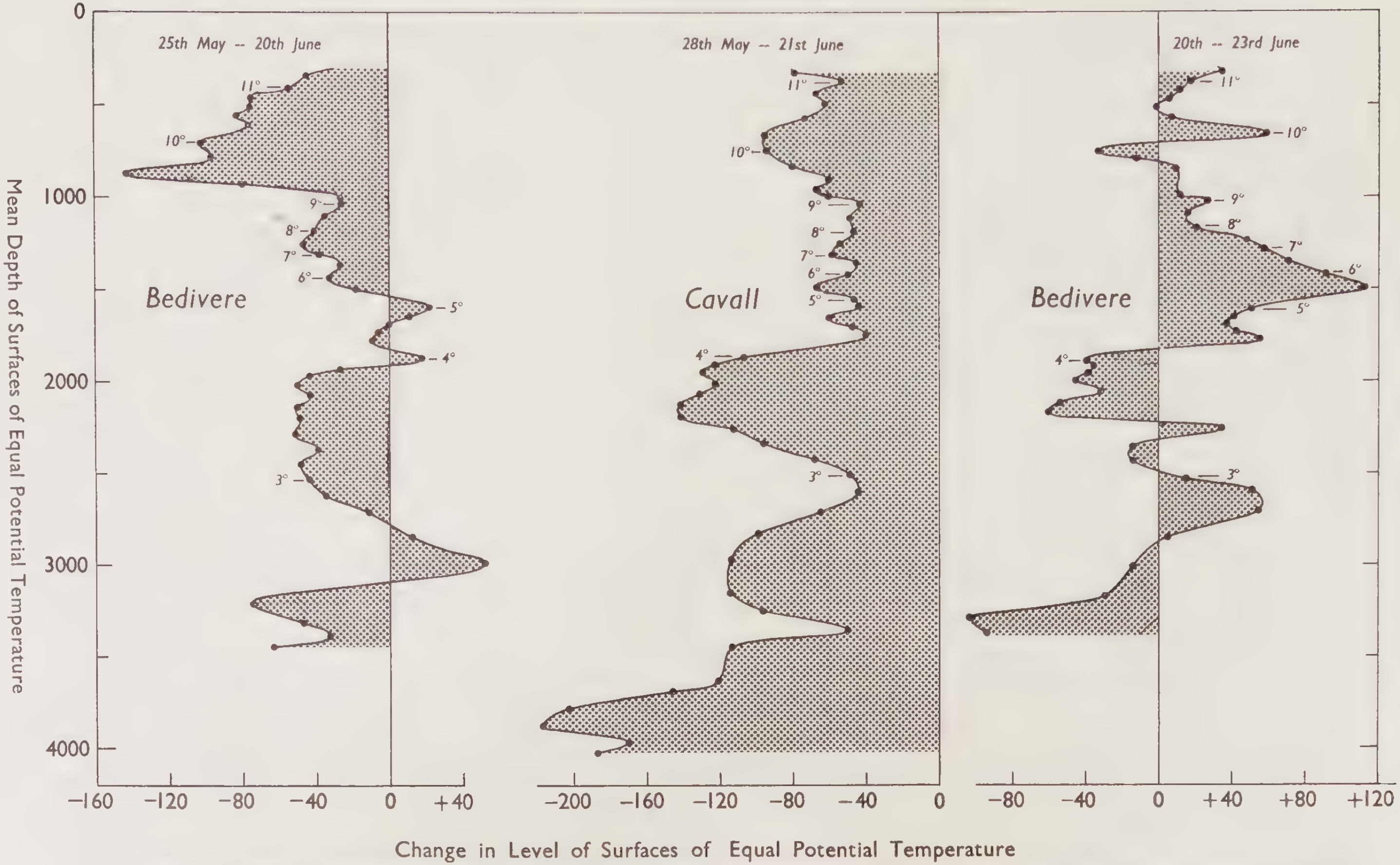

Fig. 2. Changes in level of surfaces of equal potential temperature in the Bay of Biscay, May and June 1956, plotted against weighted mean depths of the surfaces. All depths and levels in metres.

to test this hypothesis but with faint hope of separating it from error of observation. What was found was clear-cut and utterly unexpected—an upward displacement of 75 m or more of all water between 300 and 4000 m within a month (Fig. 2).

On both May and June cruises in 1956 work at station Cavall was spread over 3 days, hoists being repeated several times. Most bottles carried two protected and two unprotected thermometers. In consequence the depths of isothermal surfaces at intervals of 0·1° C potential temperature have been derived from a considerable number of independent measurements. At station Bedivere work, though less intensive, was adequate. The precision of the salinity analyses falls below the standard required for this investigation. Station lists have not yet been published.

TABLE 2. CHANGES IN DEPTH OF ISOTHERMAL SURFACES, MAY AND JUNE 1956, METRES

Depth range (m)	Cavall minus Bedivere: May	Cavall minus Bedivere: June	Cavall: June minus May	Bedivere: June minus May
300–1000	+13	+18	− 74	−79
1000–2000	+ 6	−42	− 65	−17
2000–3000	+12	−52	− 91	−27
3000–3500	− 4	−61	−101	−44
3500–4000	—	—	−166	—

The differences in level of isothermal surfaces may be compared as between the two stations in the same month or between the 2 months at the same station. First this will be done by integrating the results over thick strata (Table 2). The usual sign convention of oceanography, that depth increases positively downwards, is used.

First, it will be seen that in May (column 2) there was a small upward trend of about 10 m of the isotherms between Cavall and Bedivere down to 3000 m depth. This is trifling compared with those to be discussed.

Secondly a large surge affecting all depths to the bottom occurred at both stations between May and June (Table 2, columns 4 and 5; Fig. 2, two left-hand panels); in the deepest water at Cavall the rise in the isotherms was as much as 160 m and the rise was much greater at Cavall than at Bedivere. At Cavall there was no temperature or depth at which isothermal surfaces sank. The irregularities of the curves in Fig. 2 are due to internal waves imposed on the over-all uplift. They may be smoothed out as in Table 2.

Since the upward displacement was ten times larger than that expected and was greatest at the wrong depth, it is not evidence for the working hypothesis. There is here a new unsuspected phenomenon.

Let us first focus attention on the closed basin at Cavall at depths greater than 3800 m where the rise between May and June approached or exceeded 200 m.

First, let us assume that some kind of abyssal surge, internal wave or seiche occurred within the basin. If so the isotherms on the south-western side of the basin should have been falling while those on the north-eastern were rising. The event occurred where small changes in temperature and of salinity so nearly compensate each other that the abyssal water within very narrow limits is in neutral dynamic equilibrium. In such water it is difficult to visualize any kind of wave or seiche. Oscillations would seem to involve large changes in momentum though the energy involved must be very small, much too small to lift an overlying body of water, 3500 m thick through 70–100 m. This first assumption therefore is highly improbable.

Secondly, let us assume that a new supply of very heavy water entered the basin upwardly displacing the water already there. On this explanation, the maximum upward displacement at a mean depth of about 3900 m was about 210 m. This explanation requires rapid transport of a very large volume of water from an unknown source. It could provide the means of uplifting all the overlying water. The content of silicate does not agree with recruitment of much water from the north. The existence of the Mid-Atlantic and Walvis Ridges would make it difficult for a large scale flow of water to have come from the far south. The second assumption, in this form, is as improbable as the first. It can be modified to yield a third assumption.

Thus, thirdly, let us assume that the basin of the eastern North Atlantic may exhibit large-scale oscillations and displacements of water which affect all of it at once. The oscillations of the deepest waters would then be not a cause but a consequence of the massive displacements of the overlying more strongly stratified waters.

The least controversial explanation of the observations is therefore that within the 3 weeks between the May and June cruises we witnessed a massive oscillation of the whole of the eastern North Atlantic with a displacement of water at all depths between about 300 m and the bottom, reminiscent of the internal tide waves discussed by Defant (1950). On this view the massive oscillation was part of an equilibrium long-period tide, probably the lunar fortnightly or lunar monthly constituent (Doodson & Warburg, 1941, p. 49). In the 3 days between 20 and 23 June at station Bedivere, the movement of isothermal surfaces was predominantly downwards (Fig. 2, right-hand panel); this phasing rather favours the lunar fortnightly tide. As Defant pointed out, internal tide waves gravely interfere with the design of experiment in the deep ocean since the amplitudes of motions due to internal tides may be larger than those of the displacement phenomena we wish to study.

My hypotheses to explain the enrichment in the 1920's of the English Channel with nutrients require first that there should have been a long-period upward displacement of nutrient levels in the eastern North Atlantic, and that secondly there should have been an intensification of the internal waves beating against the continental slope. On a first appreciation the upward displacement of about 75 m in May–June 1956 provided very strong evidence. But as time passed, no consequent enrichment of the waters of the English Channel followed so that, it would seem, such massive upward displacements may be commonplace and may not provide an explanation of the enrichment of the English Channel in the 1920's.

Again, since the sea surface cannot be displaced upwards by more than a few centimetres, the upwardly displaced water had to escape as horizontal currents at depths between the surface and 300 m, so influencing the pattern of surface currents in the Bay of Biscay. If the deep oscillation was tidal, the consequent pattern of surface currents was also tidal and should be identifiable with a harmonic component in tidal analyses around southwestern Britain.

TABLE 3. CHANGE IN POTENTIAL TEMPERATURE WITH TIME

Depth	Caribbean, March 1933 to December 1954	Bay of Biscay, 28 May to 21 June 1956	Ratio: Biscay/ Caribbean
1500	+0·047	−0·45	− 9·6
1600	+0·036	−0·21	− 5·8
1750	+0·024	−0·15	− 6·3
2000	+0·015	−0·13	− 8·7
2500	+0·008	−0·08	−10
3000	+0·005	−0·08	−16

If we were dealing solely with upward displacement the concentration of oxygen, phosphate and silicate would have moved precisely with temperature. This was not so at any depth. Consequently upward displacement must have been accompanied by considerable horizontal displacement.

Worthington (1955) published observations to suggest that the deep water of the Caribbean is warming up (Table 3). By the same argument the Bay of Biscay would be cooling down very fast. The fall in temperature within 24 days in the summer of 1956 was ten times larger that the rise within 21 years in the Caribbean. Table 3 points the need for great caution in assessing long-term changes in the deep ocean from the scanty data we have.

SUMMARY

A set of 'standard' stations has been established in the Bay of Biscay and related to the grid of the Decca Navigator system. Whilst on station the ship is maintained within a circle of radius 1 mile.

In May and June 1956 repetitive hoists were made to the bottom at station Cavall (4700 m deep) and Bedivere at the foot of the continental slope. In 3 weeks there was a large upward displacement of all isotherms, averaging about 40 m at Bedivere and 80 m at Cavall, over all depths between 300 and 3500 m. The upward displacement was even greater at 3500–4000 m depth.

Oscillations in the ocean abyss and inflows at the bottom of Arctic and Antarctic waters are examined and dismissed as likely explanations. The least

controversial explanation is that a massive oscillation of the whole of the eastern North Atlantic occurred in June 1956. This may have been a long period tidal phenomenon.

At standard depths the fall in temperature in 24 days was ten times greater than changes in the Caribbean reported as evidence for long-term warming-up of the ocean.

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THE VERTICAL DISTRIBUTION OF CHLOROPHYLL[1]

By J. H. Steele[2] and C. S. Yentsch
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(Text-figs. 1–7)

The vertical distribution of chlorophyll in the sea generally shows a maximum concentration at a depth which may vary from at or just below the surface, to near or below the bottom of the euphotic zone. The easiest distributions to explain are those where the maximum chlorophyll concentration is at or very near the surface. These are found when a population is photosynthesizing actively during the first stages of an outburst, and the distribution corresponds roughly with the change with depth of the photosynthetic rate (Steele, 1957). However, these form a small proportion of observations, probably because outbursts are usually restricted to comparatively short periods of time. The more usual distributions show a maximum in the chlorophyll concentrations well below the surface and below the depth of maximum photosynthesis.

Such features are normally explained by the sinking of plants and a sinking rate constant with depth is used in the mathematical models of Riley, Stommel & Bumpus (1949) to explain some observed patterns of vertical distribution. However, on the basis of their model, the chlorophyll maximum must occur above the compensation depth. Although many of the maxima are of this type, there are as many which occur below or just at the compensation point and so are not explicable by a constant sinking rate. In particular, this feature is the dominant one in the distributions found during summer by the Woods Hole Oceanographic Institution in waters off New York (Ketchum, Ryther, Yentsch & Corwin, 1957; Ryther & Yentsch, 1958; Yentsh & Vaccaro, 1958). This work is concerned with a possible explanation for such distributions.

THE OBSERVED DISTRIBUTIONS

Two examples of chlorophyll distribution in which the maximum concentration was found near the compensation depth are given in Table 1, which includes simultaneous observations of the ^{14}C *in situ* rate of photosynthesis, and the concentrations of nitrate and phosphate in water. Crawford station

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[1] Contribution no. 1078 from the Woods Hole Oceanographic Institution. This work was supported in part by A.E.C. Contract AT (30–1) 1918.

[2] Marine Laboratory, Aberdeen, Scotland. Visiting investigator under a W.H.O.I. fellowship during the autumn of 1958.

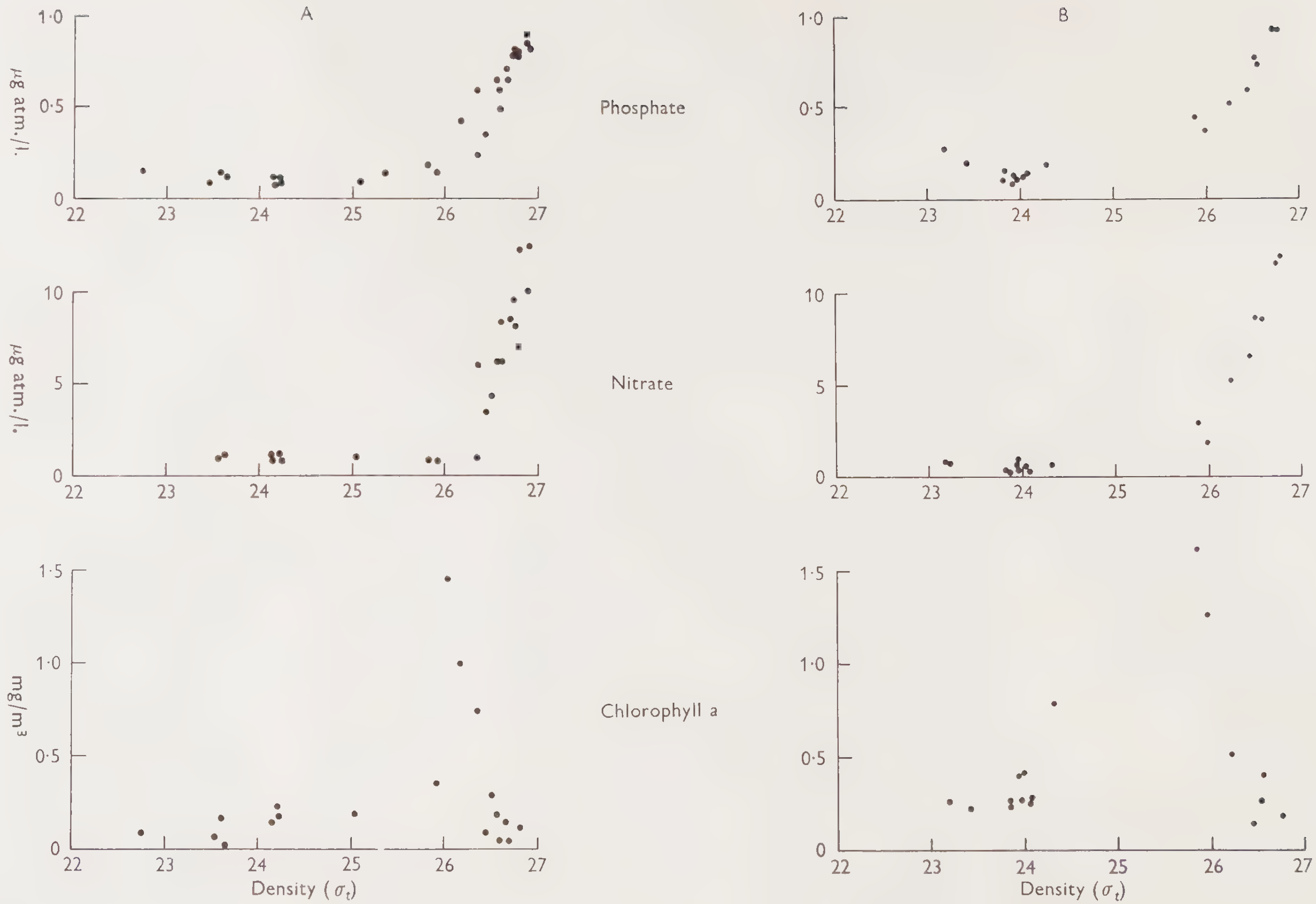

Fig. 1. Observed conditions in July (A) and September (B) 1957.

no. 194 was occupied where the total depth was 3000 m and the other station (Crawford no. 209) was in water with a depth of 40 m.

For four offshore stations in depths greater than 1000 m the relations between nitrate, phosphate and chlorophyll in July and September 1957 are shown in Fig. 1 by plotting these against density. The July chlorophyll values suggest a very sharp peak at $\sigma_t = 26$, but the September values do not have enough observations in the middle range of density to determine the sharpness. In all cases the high values are found at 50 m, although there are some stations at which no pronounced peak is found; this is probably due to the wide spacing of the sampling depths and the comparative sharpness of the peak. The occurrence of the peak in both July and September and the similarity of the nutrient distributions suggest that conditions during this interval can be considered to approximate a steady state. Perhaps the most convincing evidence that the depth of the mean daily euphotic zone is near these peaks is shown by the concentrations of nutrients which increase sharply at about the same depth. The ^{14}C data can be used to define the depth distribution of production. It appears that the compensation point at station 194 must be just below 50 m and the 1 % light level was found at 58 m. At the shallower station the compensation depth was between 20 and 30 m and the 1 % level was at 19 m.

THEORETICAL DISTRIBUTIONS

The purpose of these theoretical considerations is to show how the sinking rate interacts with other factors affecting vertical distribution of plants, and how a variable sinking rate can produce idealized distributions similar to those described above. These concepts do not explain how this decreasing sinking rate could be brought about and since the main possible explanation is in terms of the effect of density, the theoretical relations between size, shape and density will be considered.

Since sinking is only one factor which can affect the vertical distributions of plants, the effects of variations in this rate must be linked with other factors —photosynthesis and respiration of the plants, grazing by herbivores and vertical mixing of the water. These five variables have been combined in a mathematical form by Riley *et al.* (1949). Assuming a sinking rate that is constant with depth, z, the equation for a steady state is

$$A\frac{\partial^2 p}{\partial z^2} - v\frac{\partial p}{\partial z} + (w-h)\,p = 0, \tag{1}$$

where p is the plant concentration, A is the coefficient of eddy diffusivity, v is the sinking rate, w is the photosynthetic rate and h is the combined effect of grazing and plant respiration. For a maximum concentration of plants, p

$$\frac{\partial p}{\partial z} = 0 \quad \text{and} \quad \frac{\partial^2 p}{\partial z^2} = \left(\frac{h-w}{A}\right) p < 0.$$

The latter holds only for $w > h$, that is when the photosynthetic rate exceeds the combined loss due to respiration and grazing. Thus for a constant sinking rate the maximum must occur above the mean daily compensation depth. This conclusion is independent of variations with depth in grazing or mixing. (Although it can be seen from this how decreased mixing tends to increase the sharpness of the maximum.)

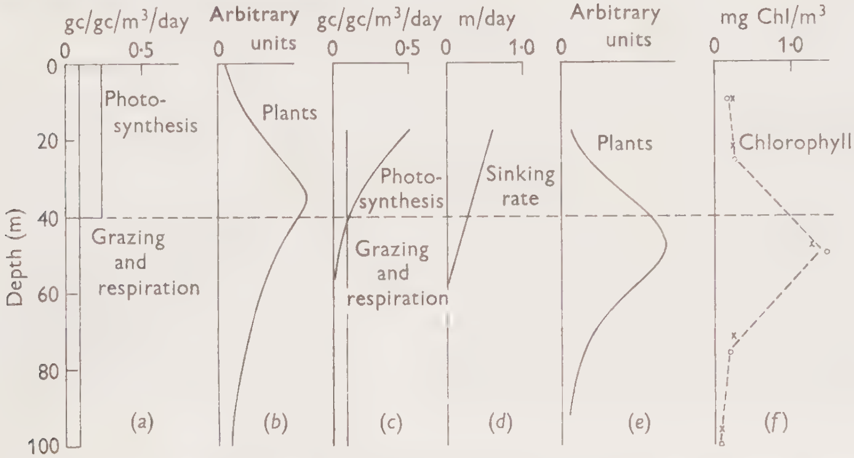

Fig. 2. (*a* and *b*) Conditions from the theory of Riley *et al.* (1949), using a constant sinking rate. (*c*, *d*, *e*) Conditions with a variable sinking rate. (*f*) Data from Station 194.

On this basis, Riley *et al.* (1949) constructed profiles of vertical plant distributions. With their solution, the deepest possible maximum will be given when a constant photosynthetic rate throughout the euphotic zone is assumed, Fig. 2(*a*). Constant sinking, grazing and respiration rates throughout the water column are assigned. With a sinking rate of 3 m day and numerical values for the other factors corresponding roughly to the offshore conditions, the example in Fig. 2(*b*) is obtained. Its disadvantage is that the form of the photosynthetic coefficient is unrealistic and biases the plant maximum downwards.

If a variable sinking rate is introduced, (1) takes the form

$$A\frac{\partial^2 p}{\partial z^2}-v\frac{\partial p}{\partial z}+(w-h-v^1)\,p=0, \tag{2}$$

where v^1 is the rate of change of the sinking rate. Then a maximum occurs when

$$\frac{\partial p}{\partial z}=0 \text{ and } \frac{\partial^2 p}{\partial z^2}=\left(\frac{h+v^1-w}{A}\right)p<0,$$

i.e. when $-v^1 > h-w$. This permits a maximum below the foot of the euphotic zone.

Thus a decreasing sinking rate is not only a possible means of securing a maximum at or below the compensation depth, which is fairly obvious; it is also the only way it can be achieved in terms of the variables considered here.

As an example of the kind of profile that can be obtained in the thermocline region offshore, a solution of (2) was constructed with a linearly decreasing sinking rate and a more realistic photosynthetic rate as shown in Fig. 2(*c*) and (*d*). The zero sinking rate has been set at 58 m so that the balance between photosynthesis and grazing plus respiration, the compensation depth of the community, occurs at nearly the same depth as in Fig. 2(*a*) and is indicated by a dashed line. This leads to the profile given in Fig. 2(*e*). The data from station 194 are shown for comparison in Fig. 2(*f*). This example shows how a decreasing sinking rate depresses the chlorophyll maximum to below the compensation depth of the community. It also provides a value for the decrease in sinking rate that is required to give a profile similar to those observed.

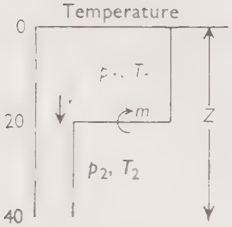

Fig. 3

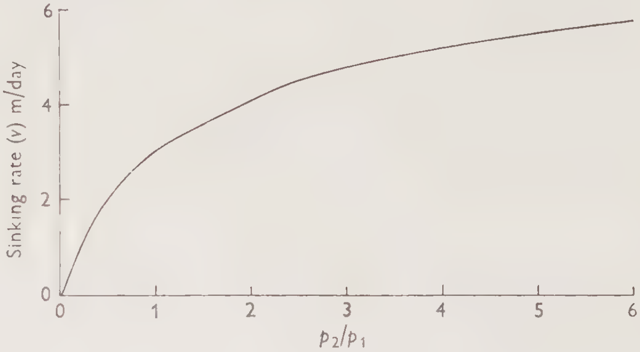

Fig. 4

Fig. 3. Idealized inshore distribution of temperature (T_1, T_2), plants (p_1, p_2), zooplankton (Z) with mixing (m) and sinking (v) between the layers.

Fig. 4. Relation between sinking rate and ratio of plant concentrations in lower and upper layers.

A second theoretical example corresponding to inshore conditions can be constructed by considering a sea 40 m deep divided into two equal layers, Fig. 3, with a positive sinking rate v in the upper layer and zero rate in the lower; this gives the relation between v and the ratio p_2/p_1 shown in Fig. 4. It can be seen that ratios of three to six which is around the observed range are obtained for a sinking rate of 5–6 m/day which is about the same value as that deduced for the upper layers in the offshore example. These values are realistic in terms of previously calculated sinking rates (Riley *et al.* 1949; Steele, 1956, 1957; Steemann-Nielsen & Jensen, 1957).

In both areas the density increase across the thermocline is in the range

0·002–0·003. From Munk & Riley (1952) the relations between the sinking rates, size of the plants, and the density difference between the plants and the water, for the simple shapes, spheres and cylinders, can be expressed approximately as

$$v_s = \frac{\Delta p d_s^2}{10} \quad \text{for a sphere (Stokes Law),}$$

$$v_c = \Delta p d_c^2 \quad \text{for a cylinder,}$$

where v_s, v_c are the sinking rates (m/day) and d_s, d_c are the diameters (μ) of spheres and cylinders, respectively; Δp is the density difference between the cell and the water.

Assuming the extreme case considered earlier, when the cells are neutrally buoyant in the lower layers, then the approximate sinking rates are obtained by putting $\Delta p = 0{\cdot}0025$. For a sinking rate of 5 m/day the required diameters are $d_s = 140\ \mu$, $d_c = 45\ \mu$. These values are high for generally observed sizes (Munk & Riley, 1952, Fig. 6) and they appear to be very much higher than those found in the areas studied. From information kindly provided by Dr E. M. Hulburt, the diameter of the main species found during the summer is generally about 5 μ and usually less than 10 μ. A value of 5 μ would give sinking rates of $v_s = 0{\cdot}006$ m/day, $v_c = 0{\cdot}06$ m/day. This is between two and three orders of magnitude less than the values calculated from the models.

THE EFFECT OF LIGHT AND NUTRIENTS ON SINKING RATES

This gross difference between the two estimates of sinking rates suggested that a change in water density alone was not a satisfactory explanation of decreasing sinking rates.[1] Thus it seemed necessary to look for changes in the density of the cells themselves as a possible explanation. It seemed probable that a decrease in sinking rate could be produced as a result of recovery of the plant cells from nutrient deficiencies. The depth at which maximum chlorophyll is observed is frequently within the thermocline, where nutrient concentrations increase with increasing depth. Gross & Zeuthen (1948) have observed variations in the sinking rates of diatoms under different culture conditions. It is a common phenomenon for the algal culturist to observe that old cultures settle out more rapidly than do young actively growing cultures.

To examine the effects of light and nutrients on the sinking rate we have conducted the following experiments. Cultures of the diatom *Skeletonema costatum* (Grev.) were grown in 4B media (Yentsch & Vaccaro, 1958) at 18° C in constant optimal light intensity. Periodically this culture was sampled and the sinking rate of the cells measured. Approximately 30 c.c. of well-agitated culture were placed in a 5 cm, large volume, optical cuvette. In the first experiment clumping was removed with a Potter–Eluehjehm homogenizer using a Teflon pestle. Optical density measurements were made in a Beckman DU spectrophotometer at a wave-length of 750 mμ. Decreases in the optical density at this wave-length, resulting from cells settling out of the light path, were measured at regular intervals over a period of 1 h (Fig. 5). The percentage decrease of the optical density during the hour is used as a measure of relative sinking rate.

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[1] Jerlov (1959) by the same reasoning given earlier noted the necessity of decreasing sinking rates to explain deep particle maxima. However, he had no information on the particle sizes and accepted density changes in the water as sufficient explanation.

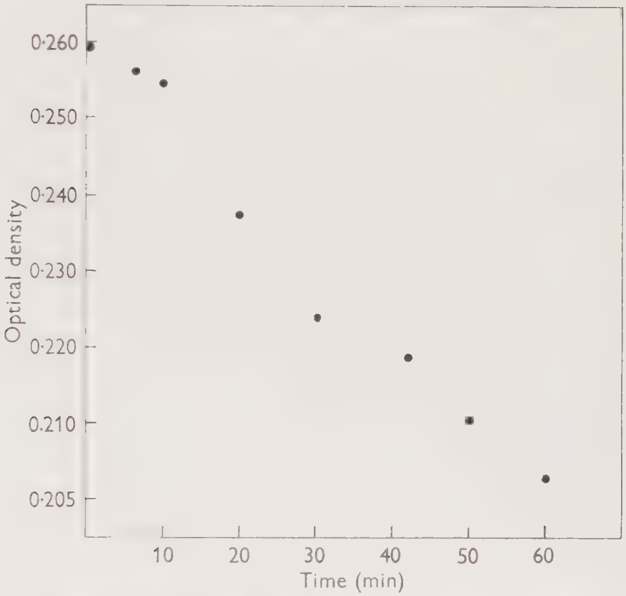

Fig. 5. Changes in optical density of a culture in a cuvette, resulting from cells settling.

The results of two experiments show that the settling rate of actively dividing cells was approximately one-half the rate of slowly dividing, senescent cells. In the first experiment, Fig. 6, an aliquot of the culture was removed between the seventh and eighth day, enriched with nutrients, and placed in the dark. During the first half day the cells in the dark settled more slowly than the illuminated cells, after which the settling rate increased.

In the second experiment three aliquots of the illuminated culture were removed between the third and fourth day of growth. Two of these were enriched, one was darkened, the other illuminated. The third aliquot was not enriched but was placed in the dark In all three aliquots the settling rate of cells was decreased relative to that of the original culture. The lowest settling

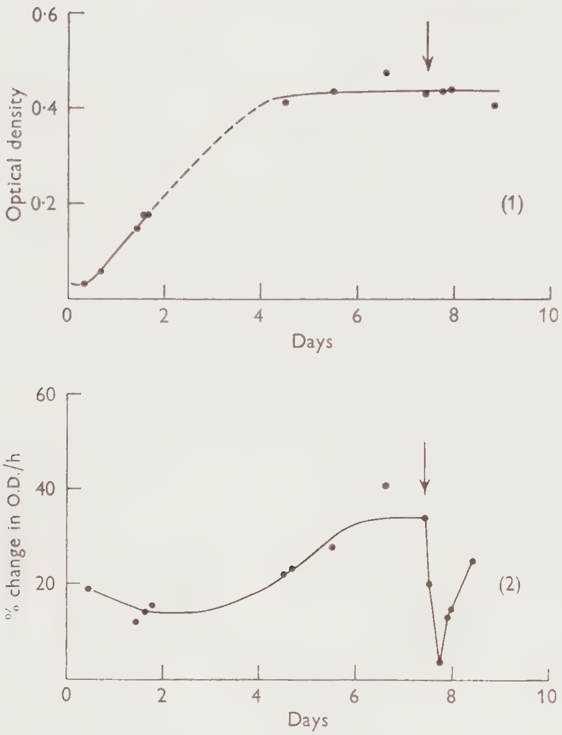

Fig. 6. Experiment I, changes with time in culture density (1) and the relative sinking rate (2). The arrows indicate the time at which 300 c.c. of 4B media was added to 150 c.c. aliquot of the culture and placed in the dark.

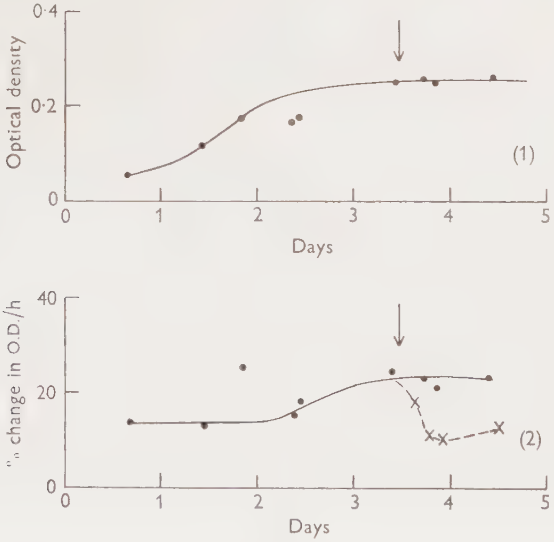

Fig. 7. Experiment II, changes with time in culture density (1) and relative sinking rate (2). The arrows indicate the time at which 300 c.c. of 4B media was added to 150 c.c. aliquot of the culture and placed in the dark.

rate occurred in the enriched darkened aliquot, Fig. 7, broken line, with the others intermediate between this and the control.

The results of these experiments show that older cells settle faster than do rapidly growing cells. Furthermore, when old cells are enriched in the dark, the settling rate is considerably reduced.

DISCUSSION

From a mathematical model which used as parameters of the phytoplankton environment, photosynthesis, respiration, grazing and eddy diffusion, we have concluded that a decreased sinking rate is needed to produce chlorophyll maxima at or below the base of the euphotic zone. Density differences observed throughout the water column appeared unable to explain these vertical distributions, and so we postulated the concept that the chlorophyll maxima are due to a decrease in sinking rate of the plants themselves caused by their entry into the dark, nutrient-rich waters found at the foot of the euphotic zone. The justification of this rather tentative hypothesis is that it predicted an experimental result.

Our experimental results show that as growth slows down, the cells sink more rapidly. When the deficient cells are re-enriched and placed in the dark, their sinking rate decreases rapidly. The picture that emerges is one where the general physiological condition of the cell and its buoyancy are closely related, as Gross & Zeuthen (1948) have also suggested. On this basis, seasonal variations in the vertical distribution of chlorophyll can be explained. For example, during early spring when nutrients are sufficient, phytoplankton cells would tend to have a low sinking rate, and populations undergoing rapid growth would tend to accumulate near the surface. In late summer when nutrients are depleted in the surface waters, phytoplankton would sink and accumulate in the nutrient rich water at the base of the euphotic zone. Here the assimilation of nutrients which can proceed in the dark (Ketchum, 1939) would, as our experiments show, decrease the sinking rate of the phytoplankton cells.

SUMMARY

Theoretical considerations of the occurrence of chlorophyll maxima at the foot of the euphotic zone show that a decreasing sinking rate is necessary to explain this feature but that the required decrease could not be obtained from density changes in the water alone. It is thought that the cells themselves might increase their buoyancy when they reach dark, nutrient-rich waters, and this has been confirmed by two experiments in which deficient laboratory cultures of *Skeletonema costatum* were re-enriched in the dark and decreased their sinking rate considerably.

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TABLE 1. EXAMPLES OF THE VERTICAL DISTRIBUTION OF CHLOROPHYLL, OF THE RATE OF PHOTOSYNTHESIS AND CONCENTRATION OF NUTRIENTS AT STATIONS WHERE THE MAXIMUM CHLOROPHYLL CONCENTRATIONS OCCURRED AT OR NEAR THE COMPENSATION DEPTH

Depth (m)	Chl *a* mg/m^3	^{14}C *in situ* measurements mg C/m^3/day	NO_3—N µg atm./l.	PO_4—P µg atm./l.
		Crawford station 194, July 1957		
10	0·18	1·8	0·53	0·09
25	0·24	5·2	0·39	0·11
50	1·46	5·6	0·43	0·19
75	0·19	0	6·00	0·59
100	0·09	0	6·20	0·66
		Crawford station 209, July 1957		
0	0·40	24·0	0·96	0·48
10	0·57	9·3	0·50	0·36
20	1·62	8·7	1·17	0·54
30	0·25	0	4·50	0·41

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UNDERWATER DAYLIGHT MEASUREMENTS IN THE BAY OF BISCAY

By B. P. Boden, E. M. Kampa and J. M. Snodgrass

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(With Plate I and Text-figs. 1–8)

As modern instrumentation improves the precision of the measurements of underwater light, particularly of monochromatic light, both biological and physical oceanographers are becoming increasingly interested in such measurements in deep water.

Two sets of observations of ambient light to depths of 400 m are presented here. It is suggested that the results were affected by both biological and physical factors.

MATERIALS AND METHOD

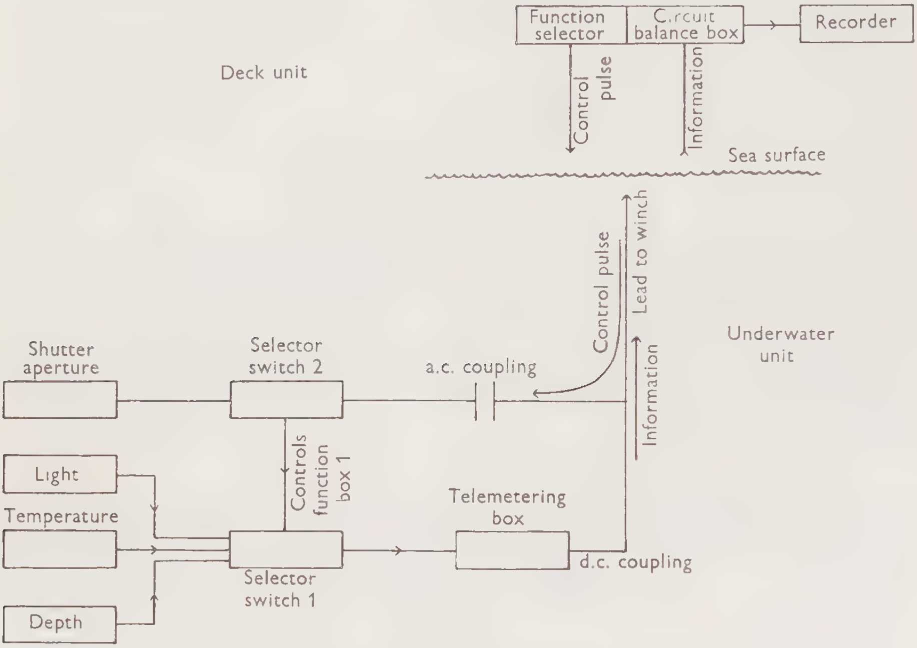
The light measurements were made by means of a telerecording bathyphotometer. There have been previous references in the literature (Kampa & Boden, 1956; Boden & Kampa, 1957, etc.) to a manuscript description of this instrument by Snodgrass, Cawley & Devereux. This account was never published and, since the instrument has now been modified, it is here described. This instrument comprises two units—an underwater unit and a deck unit.

The underwater unit (Pl. 1 A, B) is housed in a stainless-steel tube with walls ½ in. thick and consists of a photosensor (RCA 931-A multiplier phototube) with a shutter, a depth sensor, a temperature sensor, control circuits and power supply, and the telemetering circuit by which light, depth, and temperature information are transmitted. It is supported by an insulated, single-conductor cable along which the data are telemetered. There are several advantages to the use of this type of cable. It is extremely strong (breaking strain 2800 lb.) and can be wrapped on a relatively small winch (800 lb. total weight). Due to the buoyancy of the polythene insulation the weight of this cable in water is only 16 lb./1000 ft. In multi-channel cable there is always a danger of short-circuits between the conductors due to mechanical stresses on the winch or block. This is eliminated here. The system uses a sea return.

Signals from the cable are transmitted via slip-rings on the winch to the deck unit.

The deck unit (Pl. 1 C) includes the circuitry that enables the operator to select the function (light, depth or temperature) to be recorded, a number of bias circuits for zeroing the instrument, and a recorder (Pl. 1 D) to which the information is relayed.

The connexions are summarized in Text-fig. 1.


Function selector
Circuit balance box
Recorder
Deck unit
Control pulse
Information
Sea surface
Control pulse
Lead to winch
Underwater unit
Shutter aperture
Selector switch 2
a.c. coupling
Information
Light
Temperature
Controls function box 1
Telemetering box
Selector switch 1
d.c. coupling
Depth

Text-fig. 1

Circuits

Circuit diagrams for the entire instrument are shown in Text-figs. 2–4. The photometric circuitry (modified from Sweet, 1946) gives a logarithmic response over seven decades of light intensity.

The use of a pentode tube as a telemetering coupler (Valley & Wallman, 1948) obviates the interference of various potentials in the earth circuit, such as potentials between the steel hull of the ship and bronze propellor shafts and the water.

Depth

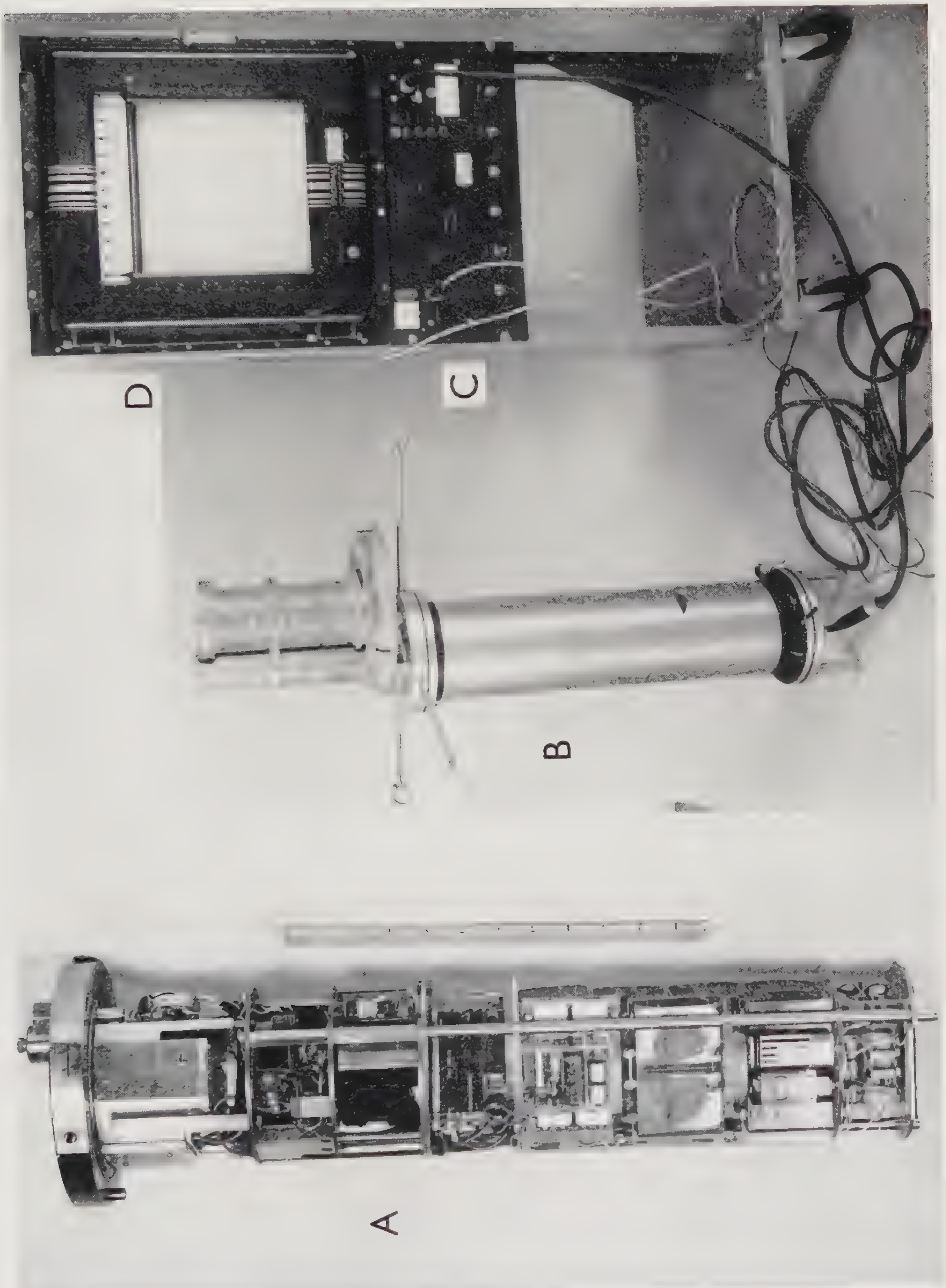
This element is a Bourdon tube coupled to a slide-wire potentiometer. It has been described elsewhere (Boden, Kampa, Snodgrass & Devereux, 1955).

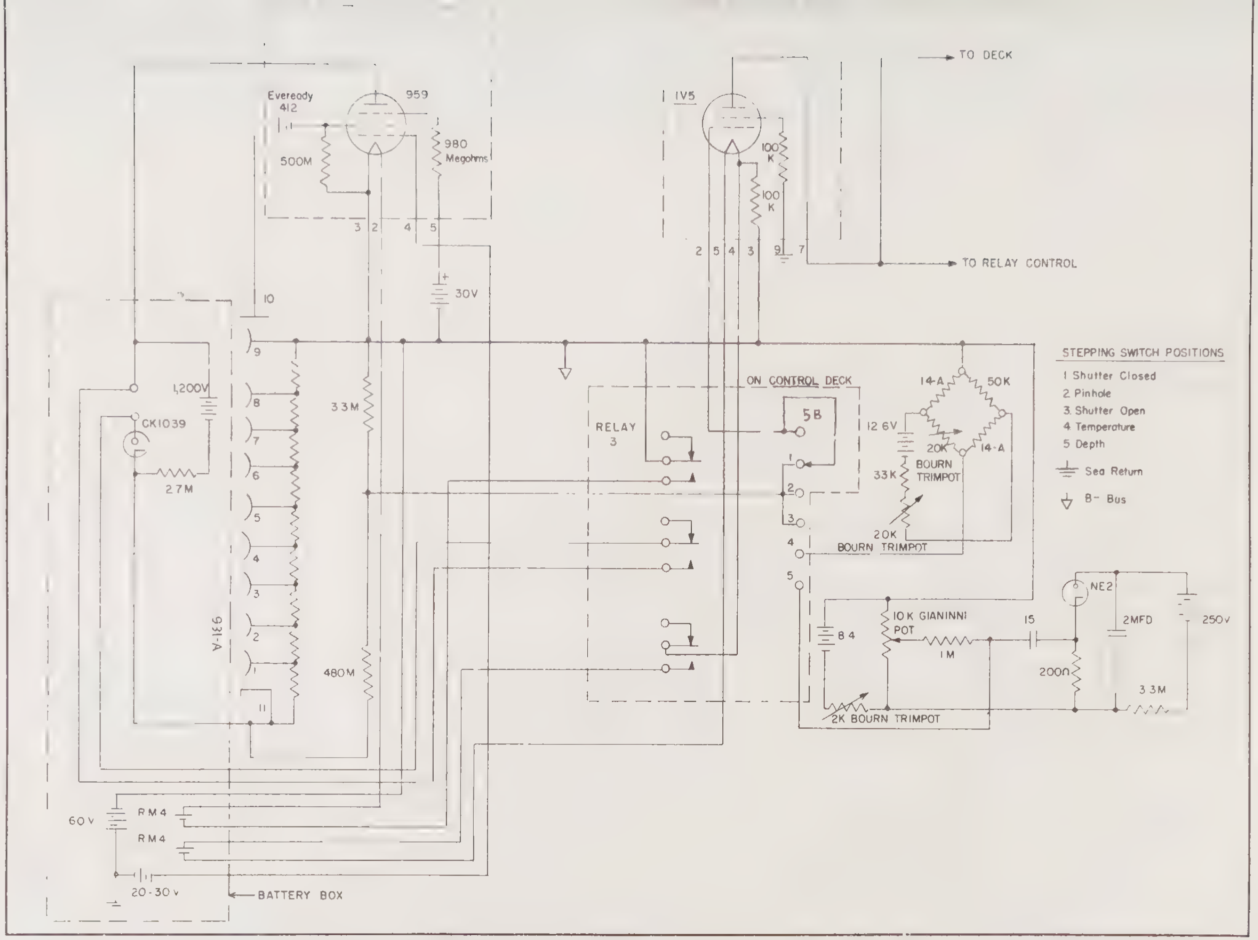
Temperature

Water temperature is measured by a matched pair of 14-A thermistors, which operate in opposite arms of a full-resistance bridge. The bridge unbalance potential is applied directly to the grid of the IV 5 telemetering tube through a stepping switch.

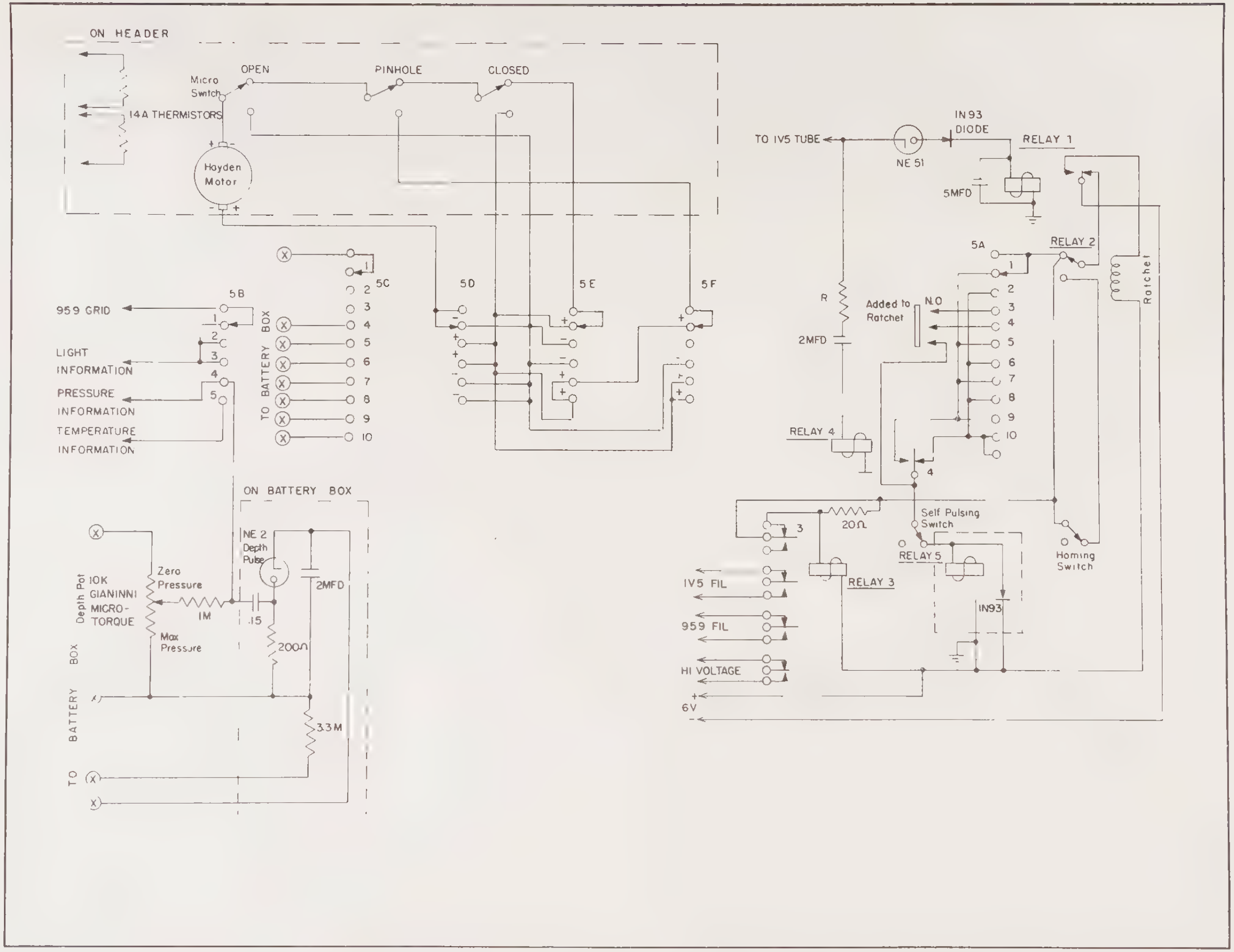
EXPLANATION OF PLATE 1

A, underwater unit of photometer without case. B, underwater unit in case with collimating tube and automatic filter changer in position. The unit is connected by a test lead to C, the deck control unit, which is connected to D, a Leeds and Northrup Speedomax recorder.

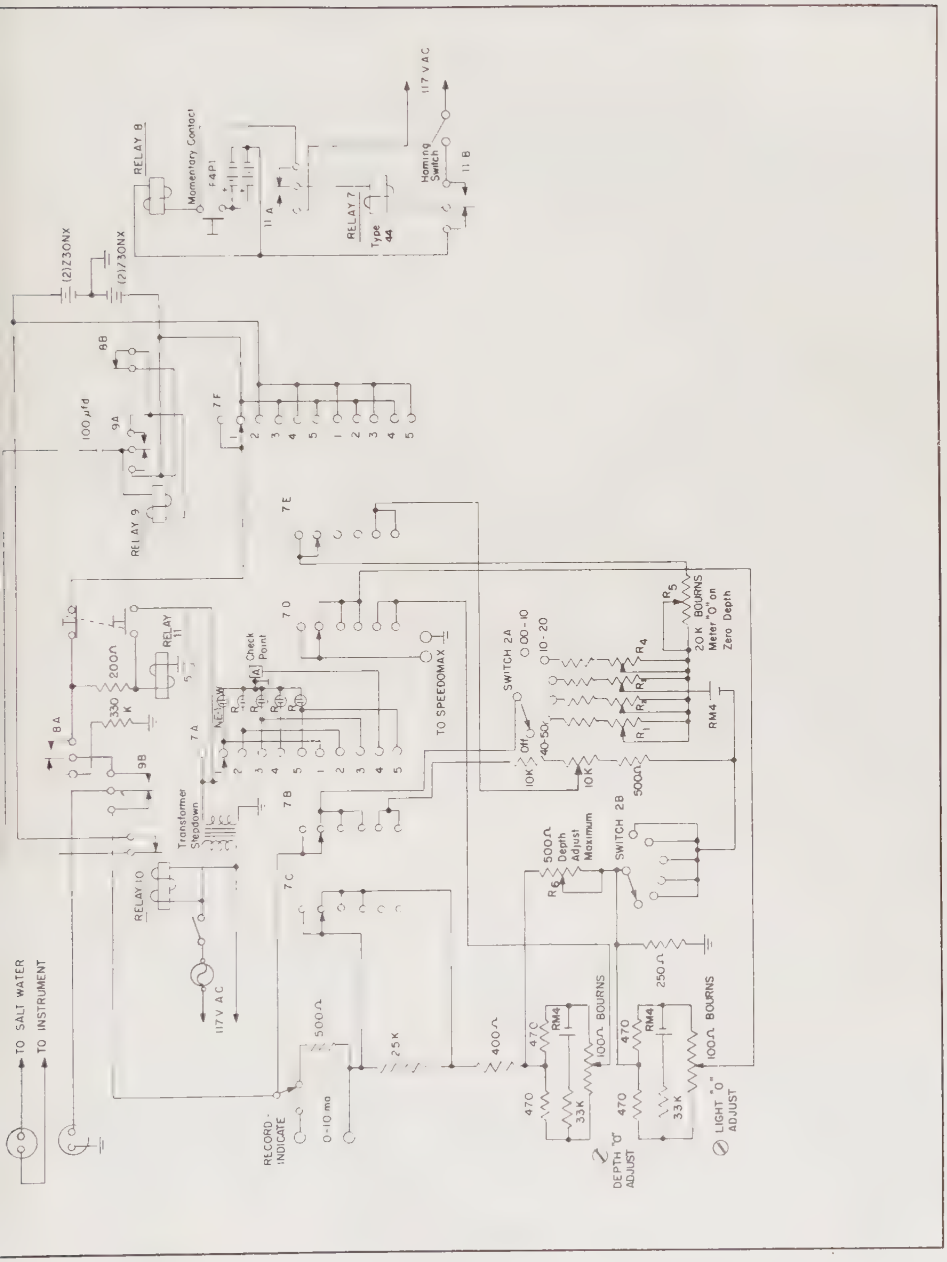

D
C
B
A


TO DECK
TO RELAY CONTROL
Eveready 412
959
500M
980 Megohms
3 2 4 5
30V
IV5
100 K
100 K
2 5 4 3 9 7
10
1,200V
CK1039
2.7M
9 8 7 6 5 4 3 2 1 11
931-A
3.3M
480M
RELAY 3
ON CONTROL DECK
5B
1 2 3 4 5
12.6V
14-A
50K
20K
14-A
33K
BOURN TRIMPOT
20K BOURN TRIMPOT
STEPPING SWITCH POSITIONS
1 Shutter Closed
2 Pinhole
3 Shutter Open
4 Temperature
5 Depth
Sea Return
B- Bus
NE2
2MFD
250V
10K GIANINNI POT
1M
15
200Ω
3.3M
8.4
2K BOURN TRIMPOT
60V
RM4
RM4
20-30V
BATTERY BOX

Text-fig. 2. Sensing circuits—depth, temperature and light. The assembly consists of the multiplier phototube (931-A) with its associated glow-type regulator (CK 1039) which is coupled to the type 959 control tube. The batteries are turned on and off from the deck unit by means of the multiple contacts on relay 3. The IV 5 tube is the telemetering coupler. The stepping switch relay 5 selects the desired function. The contacts designated under 5B constitute one deck of this stepping switch. Connected immediately to this deck are the outputs from the photomultiplier control tube, the thermistor temperature bridge, and the depth potentiometer. For interconnexion of controls see Text-fig. 3.


ON HEADER
Micro Switch
OPEN
PINHOLE
CLOSED
14A THERMISTORS
Hayden Motor
5B
5C
5D
5E
5F
959 GRID
LIGHT INFORMATION
PRESSURE INFORMATION
TEMPERATURE INFORMATION
TO BATTERY BOX
ON BATTERY BOX
NE 2 Depth Pulse
2MFD
Zero Pressure
Max Pressure
1M
.15
200Ω
3.3M
Depth Pot 10K GIANINNI MICRO-TORQUE
TO BATTERY BOX
TO IV5 TUBE
NE 51
IN93 DIODE
RELAY 1
5MFD
5A
RELAY 2
Ratchet
R
2MFD
Added to Ratchet
N.O
RELAY 4
Self Pulsing Switch
20Ω
RELAY 5
RELAY 3
IN93
Homing Switch
IV5 FIL
959 FIL
HI VOLTAGE
6V

Text-fig. 3. Shutter and relay control circuits in underwater unit. Certain sensing circuit details and relays are shown for convenience. Contact groups relating to a given relay-actuating coil use the relay number as a prefix. The following letter designates the bank of contacts on the relay, e.g. contacts 5E are controlled by relay coil no. 5 and represent the 'E' bank of contacts. Numbers opposite the contacts refer to the sequence of the contacts. A single common wire connects the IV5 telemetering tube and the relay control circuits to the deck unit. The series of contacts designated 'open', 'pinhole' and 'closed' represent limit switches which determine shutter aperture. In order to determine the function being measured and to insure continued synchronization


TO SALT WATER
TO INSTRUMENT
117 V A C
RELAY 10
Transformer Stepdown
RELAY 9
100 μfd
9A
8B
8A
9B
330 K
200Ω
RELAY 11
(2)Z30NX
(2)Z30NX
RELAY 8
Momentary Contact
F4P1
11 A
RELAY 7
Type 44
Homing Switch
11 B
117 VAC
7F
7E
7D
7A
7B
7C
NE-1
Check Point
TO SPEEDOMAX
SWITCH 2A
Off
40-50
10-20
00-10
10K
10K
500Ω
R1
R2
R3
R4
R5
20K BOURNS
Meter "0" on Zero Depth
RM4
SWITCH 2B
500Ω Depth Adjust Maximum
R6
250Ω
RECORD-INDICATE
0-10 ma
500Ω
25K
400Ω
470
470
33K
100Ω BOURNS
DEPTH "0" ADJUST
LIGHT "0" ADJUST

Text-fig. 4. Deck control unit. The same designations are followed as in Text-fig. 3. In order to indicate the function being measured and to insure synchronization between deck and underwater units, two identical stepping switches are pulsed in series. These are relays 5 (in the underwater unit) and 7 (in the deck unit). To insure the operator's safety an isolating step-down transformer is used between the circuits and the 117 V a.c. power supply. Numerous range-adjusting and balancing networks are incorporated for convenience of read-out. A ground symbol indicates a good sea-water contact. The string of neon lamps connected to contacts 7A indicate the function being measured.

The stepping switch controls shutter position and also permits programmed telemetering of light, depth and temperature, or continuous recording of any selected single function.

Light

The 931-A multiplier phototube is selected for high sensitivity and low dark current. About one in five tubes tested will detect intensities as low as $10^{-5}\mu$W/cm^2 at 420 mμ when a narrow band (half-band width 10 mμ) interference-type filter is used.

The 959 electronic control tube automatically adjusts the sensitivity, and prevents damage when the instrument is exposed to bright light.

The photocathode faces outward through a synthetic sapphire window. Between it and the window is an electrically operated ribbon shutter which is controlled from the deck unit. It is possible to select one of three positions: open, closed, or pinhole. The pinhole is 0·001 the size of the open window and permits work near the surface at high intensities. This increases the useful range of the instrument to ten decades of light intensity. With the shutter closed it is possible to measure the dark current of the photomultiplier when the instrument is at depth.

Outside the sapphire window is an optical system through which the sea water passes freely. A battery-operated, automatic filter-changer places interference filters in this system for colour measurements. The filters are placed between the sapphire window and a free-flooding collimating tube that restricts the acceptance angle of the filters to its useful 5° cone. At the distal end of the collimating tube is an integrating disc of opal plastic material with the characteristics of a true cosine collector. Thus the instrument measures irradiance.

Calibration of the photometer

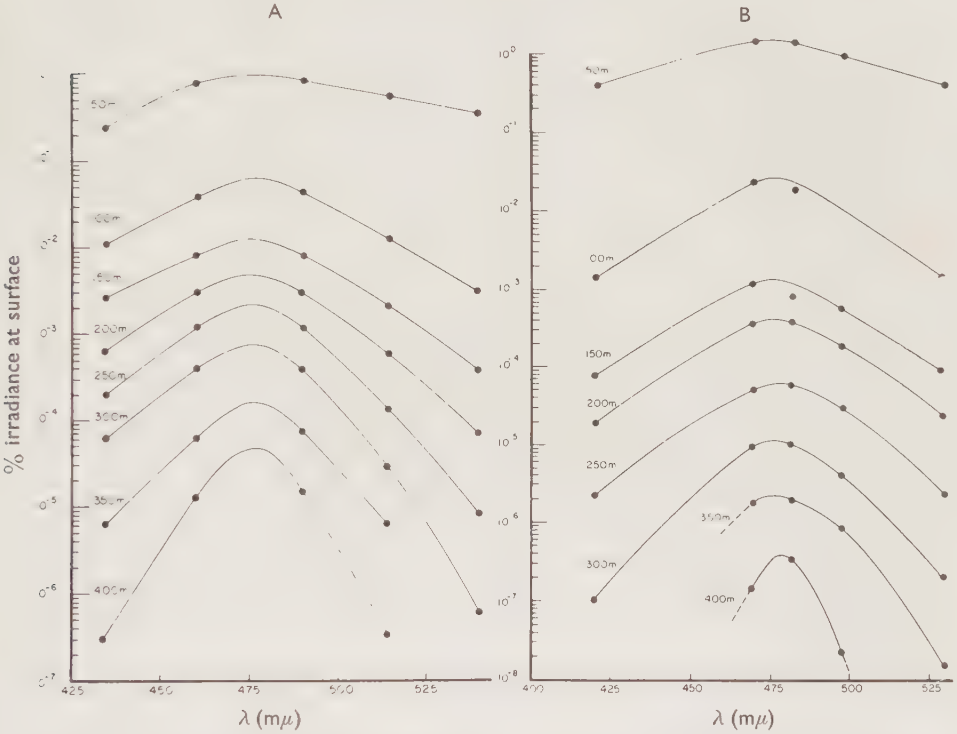
For each filter, curves giving deflexion against incident flux were constructed by attenuating in known steps the light falling on the bathyphotometer from a constant light source and measuring the deflexion of the recorder. The light was attenuated by calibrated neutral filters and by varying the distance between the light source and the instrument. If now for a given filter the deflexions of the recorder are found with the bathyphotometer at the surface of the sea and at a depth z, the diminution of the irradiance from the surface to depth z, for the narrow band of wavelengths transmitted by the filter can be found.

The instrument was also calibrated for absolute energy levels as follows. A calibrated light source (a tungsten filament lamp supplied by the U.S. Bureau of Standards and run at a constant voltage) was used to give a known energy distribution in W/cm^2/mμ striking the opal of the bathyphotometer. The deflexions given by the recorder of the bathyphotometer were then measured for each of the filters in turn. For any other set of lighting conditions the deflexions given by the bathyphotometer with the same filters can be found. It is now possible, using these results together with the curve showing, for each filter, deflexion against intensity of light, to compare the unknown with the known energy distributions. In this way a curve giving irradiance (H_λ) in W/cm^2/mμ against wavelength (λ) can be found. The integral $\int H_\lambda\, d\lambda$ over the spectrum gives the total irradiance. This calibration is valid for lights in which the spectral distribution of energy is broad compared with the narrow bands of transmission of the filters. This is true for the measurements of penetration of light into the sea desired here.

RESULTS

The results reported here were obtained at Station Cavall in the Bay of Biscay (lat. 46° 29′ N., long. 7° 59′ W.) on 25 September 1958, from the Plymouth laboratory R.V. 'Sarsia'. Station Cavall is one of several hydrographic stations established by Dr L. H. N. Cooper during his investigation of this area, and it was occupied for several days at this time.

The bathyphotometer was lowered twice during the day. The morning cast was made between 10.30 and 11.30 h and the afternoon cast between 13.25 and 14.10 h. The interference filters used in the morning cast had pass bands with peaks at 434, 460, 491, 514 and 540 mμ. Those used in the afternoon transmitted maximally at 421, 470, 482, 498 and 528 mμ.



Text-fig. 5. Spectra of transmitted sunlight at 50 m intervals of depth in the Bay of Biscay (lat. 46° 29′ N., long. 7° 59′ W.) on 25 September 1958. A, 10.30–11.30 h G.M.T.; B, 13.25–14.10 h G.M.T.

At this latitude, at this time of the year, differences in degree of underwater irradiance due to differences in the sun's altitude at periods as closely spaced as these during the middle of the day are less than 5%. However, sky conditions changed between the two casts. In the afternoon a light, high haze caused some forward scattering. The afternoon irradiance values are higher than those obtained in the morning, but this is not a matter of importance, since the values have been equated to 1 at the surface, and only relative values are considered.

The spectral composition of the light at 50 m intervals to a depth of 400 m is shown in Text-figs. 5 A, B. The distribution obtained in the morning is very similar to that obtained in the afternoon, although different sets of filters were used. The light becomes steadily bluer with depth until at 400 m the spectrum peaks sharply between 475 and 480 mμ. This is an excellent illustration of the ocean acting as a monochromator as described by Tyler (1959). These results agree closely with those obtained by Jerlov (1951) and the main interest attached to them is: (i) the relatively great depth attained, (ii) the use of a series of interference filters, and (iii) the fact that, with the automatic filter changer, the time intervals between the determinations at different wavelengths were remarkably short (10 s).

Curves depicting the penetration of daylight of various wavelengths are shown in Text-fig. 6 (morning cast) and Text-fig. 7 (afternoon cast). Values of the extinction coefficient (k) for each wavelength at different depths are shown in Table 1. The extinction coefficient at depth z is defined by the equation

$$k_\lambda = \ln H_{\lambda, z} - \ln H_{\lambda, (z+1)},$$

where $H_{\lambda, z}$ and $H_{\lambda, (z+1)}$ represent irradiance values of wavelength (λ) on horizontal surfaces at depths z and $(z+1)$ m.

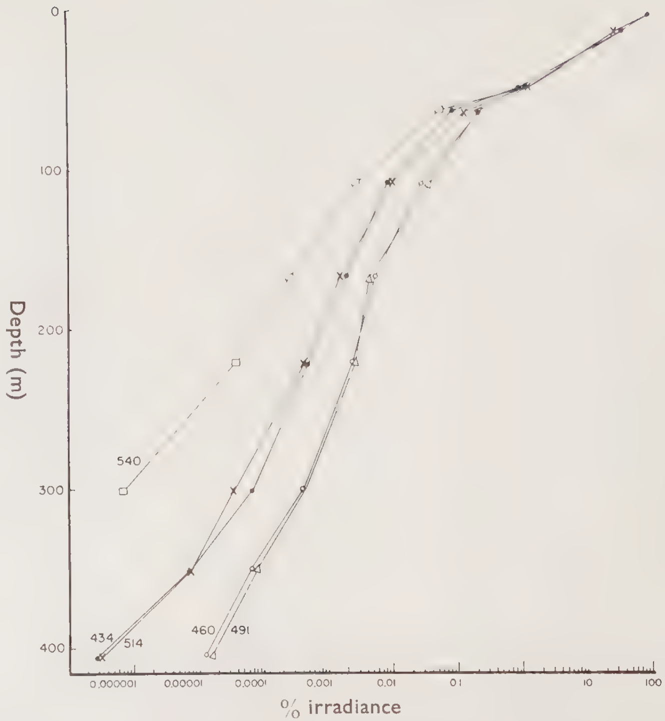
These results resemble those reported by Kampa (1955). There is a surface stratum in which extinction is rapid. This overlies a thick layer of very transparent water. Somewhere below 300 m a further inflexion suggests that the water becomes optically denser than that just above it.

In the morning cast a layer (between 45 and 60 m) was detected, between the optically dense surface water and the more transparent deeper water, which was very much more opaque than the surface water (for example, $k_{541\,\mathrm{m}\mu} = 0{\cdot}221$, which is about the average extinction coefficient for coastal waters according to Utterback's (1936) data).

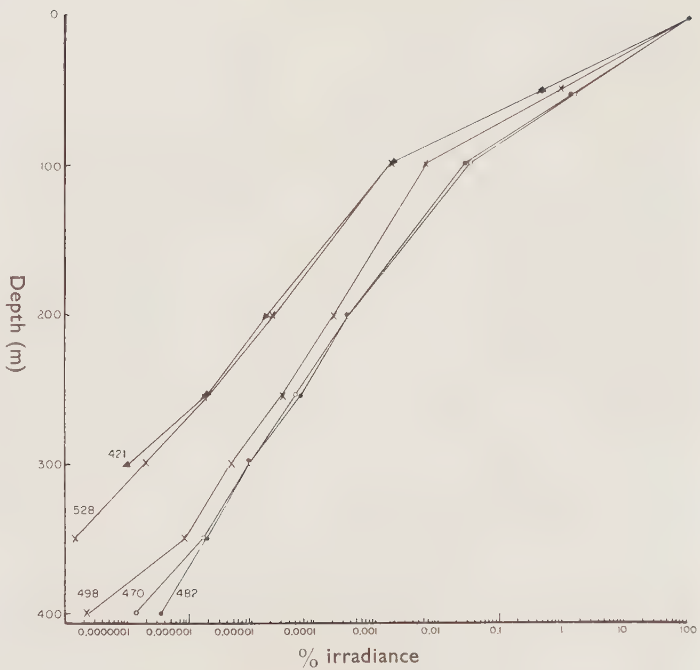
This micro-layer was not demonstrated by the afternoon cast, and the break between the surface layer and the middle layer had sunk to about 100 m.

Dr L. H. N. Cooper (personal communication) has kindly supplied us with the data showing the vertical thermal structure (Text-fig. 8) at the time of the casts. Our thermistor circuit failed during the operation, and we did not record temperature. It can be seen that there was a very strong thermocline somewhere between 40 and 97 m. Correlations between attenuation coefficients and thermoclines in the north Pacific have been reported by M. Koslyaninov (Academy of Sciences, U.S.S.R.—personal communication to Mr J. E. Tyler, Scripps Institution).

Between the morning and afternoon casts the wind had increased from force 3 to force 4 and the sea from state 3 to state 5. The ship drifted less than 6 miles between casts and the possibility that this resulted in the sampling of different water masses at an oceanic station is slight.



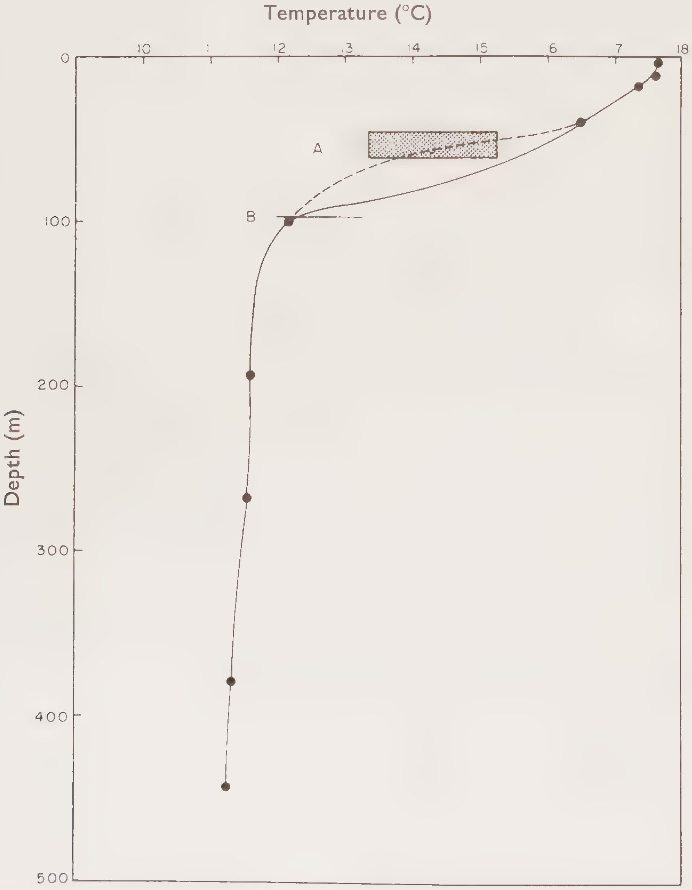
Text-fig. 6. Relation between depth and irradiance at various wavelengths expressed as percentage of irradiance values at the surface. The numbers at the ends of the curves indicate the wavelengths (in mμ) of maximum transmission of the interference filters used.



Text-fig. 7. Relation between depth and irradiance at various wavelengths expressed as percentage of irradiance values at the surface. The numbers at the ends of the curves indicate the wavelengths (in mμ) of maximum transmission of the interference filters used

TABLE 1. EXTINCTION COEFFICIENTS (*k*) OF LIGHT OF DIFFERENT WAVE-LENGTHS (λ) AT DIFFERENT DEPTHS AT STATION CAVALL

λ (mμ)	*D* (m)	*k*	*D* (m)	*k*	*D* (m)	*k*
			Morning cast			
540	0–60	0·126	60–300	0·047	—	—
514	—	0·112	—	0·034	300–405	0·045
491	—	0·102	—	0·026	—	0·032
460	—	0·101	—	0·026	—	0·033
434	—	0·118	—	0·031	—	0·052
			Afternoon cast			
421	0–98	0·111	98–300	0·048	—	—
470	—	0·081	98–350	0·039	350–400	0·050
482	—	0·083	—	0·037	—	0·035
498	—	0·096	—	0·035	—	0·072
528	—	0·111	—	0·047	—	—



Text-fig. 8. Thermal structure at Station Cavall. The stippled area A shows the vertical position of the turbid micro-layer observed in the morning. The line B shows the vertical position of the inflexion of the sunlight transmission curves in the afternoon. The positions of the thermocline in the morning (broken line) and afternoon (solid line) are inferred from the optical data.

We interpret this apparent destruction of the optically dense micro-layer and the sinking of the break between the surface and middle layers as being due to turbulence associated with this change in the weather. The high extinction coefficients in the surface layer could well have been caused by particulate matter due to the higher productivity of the layer. The vertical extent of this layer is consistent with the depth of the 'photic' zone (Hedgpeth, 1958) at this latitude. The sharp difference in the optical properties of the two layers was probably due to an accumulation of particulate matter at an interface associated with an apparently long-established thermocline.

TABLE 2. OXYGEN VALUES AT DIFFERENT DEPTHS AT STATION CAVALL

	Oxygen		
D (m)	ml./l.	% sat.	Defect (ml./l.)
97	5·52	93·6	0·37
100	5·45	94·8	0·30
193	5·57	94·6	0·32
268	5·59	95·0	0·29
381	5·38	90·7	0·55
442	5·32	89·6	0·62
537	5·02	83·9	0·96

Such turbulence would cause a slight sinking of the thermocline and this change in thermal structure is summarized in Text-fig. 8. The broken line shows the probable position of the thermocline in the morning, and the solid line the same in the afternoon. The shaded area (A) represents the turbid micro-layer present in the morning, and a line (B) shows the break between the optical properties of the upper and lower layers in the afternoon. This increase in the vertical extent of the surface layer would result in a greater dilution of the particles in it, and this is revealed by somewhat lower extinction values in this layer in the afternoon. The differences in extinction coefficients between the middle and lower layers, somewhere below 300 m, are less pronounced.

In California, Kampa (1955) found that the lower inflexion in the extinction curve was associated with the top of a sonic-scattering layer and inferred that this increased extinction was also of biological origin. We have no evidence of the existence of a sonic-scattering layer at Station Cavall at this time, but this does not preclude the possibility that one was present. The echo-sounder on the 'Sarsia' operates at a much shorter ping-length than most American instruments, and may well have not recorded a layer of the type found in California.

Cooper, who supplied the oxygen data in Table 2, writes 'between 268 and 391 m there was some evidence, particularly from oxygen, of a change in properties. It was not very marked, however'. It is apparent that the photometer entered a water mass with different optical properties at about this depth. Whether such changes in oxygen content and transparency are linked with some biological phenomenon is a moot point. There were no marked changes in temperature, salinity, or other properties at this depth.

This work was done under contract between the U.S. Office of Naval Research and the University of California. A grant-in-aid was made by the U.S. National Science Foundation. Part of the work was supported by the U.S. Bureau of Ships.

We wish to thank the Director, Dr F. S. Russell, F.R.S., for the unfailing hospitality of the Plymouth Laboratory, the scientific staff of the laboratory and the captain, officers and crew of the R.V. 'Sarsia' for their help under rather trying circumstances. Dr L. H. N. Cooper, for whom the cruise was scheduled, was extremely generous in granting us time and in making available the pertinent hydrographic data.

SUMMARY

A telerecording bathyphotometer embodying a multiplier phototube is described and the circuitry is illustrated. Measurements were made of the penetration and spectral characteristics of daylight to a depth of 400 m in the Bay of Biscay. It is suggested that the rapid attenuation of light in the upper 100 m was due in part to biological matter associated with a sharp thermocline. A change in the weather is presumed to have caused a change in the depth of the thermocline and this is reflected in a change in attenuation coefficients.

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Printed in Great Britain

CARBOHYDRATES IN SOME MARINE PLANKTONIC ANIMALS

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There have been few analyses of the fat, protein and carbohydrate fractions in zooplankton, and owing to the difficulty of sorting large numbers of single species, the majority of the earlier determinations were necessarily carried out on mixed zooplankton hauls (Brandt, 1898; Brandt & Raben, 1919; Moberg, 1926; Wimpenny, 1929; Drummond & Gunther, 1934; Vinogradov, 1953). Most of these analyses suggested a relatively high protein and fat content, and this was confirmed by Orr (1934*a*), who investigated the chemical composition of a single species, *Calanus finmarchicus*. Orr's result gave fat, protein and chitin as 20–40, 35–50 and 3 %, respectively of dry weight. Similar high values were also reported by Orr (1934*b*) for *Euchaeta norvegica*. The carbohydrate content was not, however, estimated in either of Orr's investigations since large numbers of animals would have been required. Brandt (1898), after analysing mixed plankton hauls which were predominantly copepods, suggested a carbohydrate content of *ca*. 20 %.

Although many workers have suggested that fat is used as substrate during the respiration of zooplankton, the role of carbohydrate is doubtful, since there is so little information on the glycogen content and on the amount of monosaccharides in plankton animals. Lane, Posner & Greenfield (1952) and Greenfield (1953) reported very high glycogen values in prenatal larvae of *Teredo*, and noted a sharp reduction in the amount in free-swimming larvae. Collyer (1957) found the glycogen reserves in the larvae of *Ostrea edulis* to lie between 13·4 and 15·4 % of the dry organic matter, but found no correlation with size. It therefore appeared highly desirable to investigate the total carbohydrate content (i.e. glycogen and monosaccharides) in certain planktonic animals. It also was of interest to test whether the amount of carbohydrate varied with feeding and activity, since this might indicate whether carbohydrate was normally used as an energy source.

MATERIAL AND METHODS

Experiments were carried out with *Calanus finmarchicus* (Gunnerus)[1] and *Neomysis integer* (J. V. Thompson) at Plymouth, and with *Pleurobrachia pileus* (O. F. Müller) at Southampton. In each case the animals were picked out from diluted plankton hauls. In the experiments with *Calanus*, over 100 animals were used for each carbohydrate determination. For experiments where the animals were first fed, batches of fifty animals were sorted into beakers, each containing a litre of filtered sea water enriched with cultures of diatoms and dinoflagellates. The beakers were placed in a light-tight box in a constant-temperature room at 12° C. For starvation experiments, batches of fifty animals were kept in tall rectangular Perspex vessels (50 × 7·5 × 3·5 cm) containing filtered sea water. These vessels, set up in the constant-temperature room (12° C), were supplied with fluorescent lighting from the top and side. This lighting was used as a stimulus to keep the animals active. The copepods were usually observed to be swimming upwards.

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[1] It is likely that since these specimens were collected in the English Channel they should be referred to the variety *helgolandicus*.

In the experiments with *Neomysis*, the same procedure as described for *Calanus* was followed, except that only twenty to fifty animals were used for each carbohydrate determination. With *Pleurobrachia* three to ten animals, depending on their size, were used. Owing to the high water content, the use of greater numbers of *Pleurobrachia* was of no advantage. A few experiments were attempted using dried *Pleurobrachia*, but as it was likely that the high salt content interfered with the analyses, those experiments were not continued.

The total carbohydrate content was determined by the micro-method of Mendel, Kemp & Myers (1954) and of Kemp and Heijningen (1954). Glycogen in the tissues was first hydrolysed to glucose, the final determination (made by a colorimetric method), including any glucose and fructose originally present as monosaccharides, and also saccharides yielding those sugars. Before each analysis the animals were concentrated by filtering through bolting silk, quickly rinsed with distilled water, and roughly dried on filter-paper. Except in the case of *Calanus*, the wet weight of the whole sample was then obtained. The animals were ground with 5 c.c. of 5% trichloracetic acid containing 0·2% silver sulphate. After boiling for 15 min and then centrifuging, a clear supernatant was obtained. To 1 c.c. of this fluid, 3 c.c. of concentrated H_2SO_4 (May & Baker, 98%, sp.gr. 1·84) was added and the mixture boiled for 6·5 min to develop colour. The intensity of the resulting pink colour was measured in a Unicam spectrophotometer (SP. 600) at 520 mμ. Usually three determinations were made on each sample; the agreement between the subsamples was good. The mean value was then converted into glucose units from a calibration curve, this curve being linear between 50 and 150 μg. glucose. Values below 50 μg. could not, however, be read with accuracy.

RESULTS

Calanus

The results of a few experiments with *Calanus*, mostly Stages V and VI ♀♀, suggested a rather low concentration of carbohydrates in the body (Table 1). Most of the determinations were made on copepods which had been kept in the laboratory and were either fed or starved, but in Expt. nos. 9 and 10 analyses of freshly caught *Calanus* were made and gave values of 1·7 and 1·4 μg sugar as glucose per copepod (Table 1). Copepods which were fed on phytoplankton in the laboratory gave rather variable carbohydrate contents (viz. 2·24–0·63 μg per copepod), and the same was true of those *Calanus* which were starved, though the values then tended to be lower (1·76 to < 0·25 μg per copepod). There is thus the suggestion that starvation (with continued activity of the copepods) tended to reduce carbohydrate, whereas feeding appeared to build up a small carbohydrate reserve. It is probable that the rise in body sugar with feeding would have been clearer, and the results less variable, had feeding been really active. Many workers, notably Marshall & Orr (1955), have commented on the variability of feeding activity seen in *Calanus* kept in the laboratory. In our experiments it appeared from a qualitative examination of the faecal pellet production that the *Calanus* were not feeding actively.

TABLE 1. CARBOHYDRATE CONTENT OF *CALANUS FINMARCHICUS*

Expt. no.	No. of animals used	Carbohydrate per copepod (μg)	% carbohydrate per wet weight	Remarks
1	125	2·24	0·18	Fed
2	125	1·76	0·14	Unfed
3	200	0·41	0·03	Unfed
4	200	1·15	0·09	Unfed
5	150	1·10	0·09	Fed
6	250	0·72	0·06	Fed
7	130	0·63	0·05	Fed
8	200	< 0·25	< 0·02	Unfed
9	140	1·70	0·13	Fresh animals
10	200	1·40	0·11	Fresh animals

In these preliminary experiments the *Calanus*, though counted, were generally not weighed. In Expt. no. 9, however, with freshly caught animals, the *Calanus* were weighed after roughly drying on filter-paper, and gave a mean of 1·26 mg per copepod (wet weight). This value (1·26 mg) has been used as a first approximation to convert the weight of carbohydrate per copepod to carbohydrate per body weight (Table 1). It then appears that in freshly caught *Calanus* carbohydrates amount to 0·11–0·13 % of the body (wet) weight. According to Marshall & Orr (1955) the water content of female *Calanus* is 78 % and that of Stage V 65 %. On the assumption of 70 % water content for a mixture of females and Stage V copepodites, the carbohydrate content of freshly caught *Calanus* expressed as percentage dry weight would be

$$0{\cdot}12 \times \frac{100}{30} = 0{\cdot}4\,\%.$$

In starved copepods the maximum carbohydrate (wet weight) was 0·14% and the minimum as low as < 0·02%. For fed copepods the values were slightly higher: range 0·18–0·05% of the body (wet) weight (Table 1).

Neomysis integer

It was possible to carry out rather more experiments on *Neomysis* and in all determinations the wet weight of the animals was first obtained. The results of experiments on animals which had been fed in the laboratory gave values of 0·42–0·20% sugar as glucose of the body (wet) weight. There was again the difficulty that although *Neomysis* fed on phytoplankton cultures, the intensity of feeding, as judged from faecal pellet production, appeared to be variable. Different periods of feeding were tried, but the intensity still varied considerably. It is of interest that the highest carbohydrate content (0·42%) was obtained in Expt. no. 13 (Table 2) where particularly marked feeding was noted.

TABLE 2. CARBOHYDRATE CONTENT OF *NEOMYSIS INTEGER*

(Fed Animals.)

Expt. no.	Wet weight (mg)	% carbohydrate per wet weight	% carbohydrate per dry weight
11	160·0	0·31	1·55
12	142·0	0·20	1·00
13	180·4	0·42	2·10
14	353·4	0·22	1·10
15	243·6	0·24	1·20
16	228·0	0·28	1·40
17	251·0	0·23	1·15
18	208·0	0·22	1·10
19	310·0	0·25	1·25
20	276·7	0·20	1·00
21	318·8	0·22	1·10
22	980·0	0·22	1·10
23	389·2	0·29	1·45
24	403·0	0·26	1·30
25	333·3	0·23	1·18
26	278·0	0·39	1·95

The percentage of carbohydrate found in unfed *Neomysis* tended to be somewhat lower than in fed animals, though the range was considerable, viz. 0·28–0·15% glucose per body (wet) weight (Table 3). This suggests that carbohydrate is utilized to some extent with activity, and is stored during feeding. A somewhat closer comparison is possible for fed and unfed *Neomysis*, however. In some ten experiments the starved and fed cultures were set up simultaneously as paired experiments (Table 4). Only in one experiment (Expt. no. 28) was a greater percentage of glucose found in starved than in fed animals. In several of the pairs of determinations the reduction in carbohydrate with starvation was considerable (e.g. Expt. nos. 11 and 27, *ca.* 50%; Expt. nos. 13 and 29, *ca.* 40%), but in other experiments there was little or no change. In one of these experiments showing little change

(Expt. no. 33) duplicated unfed *Neomysis* cultures gave 0·21 and 0·24% carbohydrate against 0·23% for the fed animals (Expt. no. 17). But in the two unfed cultures, of a total of 300 mysids originally sorted, only 212 were recovered after 48 h starvation, although only a single intact dead mysid was seen. On closer examination several *Neomysis* were observed to be feeding on fragments of other mysids, suggesting that extensive cannibalism had occurred.

TABLE 3. CARBOHYDRATE CONTENT OF *NEOMYSIS INTEGER*

(Unfed animals.)

Expt. no.	Wet weight (mg)	% carbohydrate per wet weight	% carbohydrate per dry weight
27	190·0	0·15	0·75
28	161·6	0·28	1·40
29	444·2	0·16	0·80
30	389·2	0·20	1·00
31	258·7	0·20	1·00
32	251·0	0·25	1·25
33*a*	334·2	0·21	1·05
33*b*	305·5	0·24	1·20
34	392·0	0·17	0·85
35	398·4	0·27	1·35
36	455·5	0·20	1·00

TABLE 4. A COMPARISON OF THE CARBOHYDRATE CONTENT OF FED AND UNFED *NEOMYSIS INTEGER*

(The pairs of experiments cited were set up simultaneously.)

Fed		Unfed	
Expt. no.	% carbohydrate per wet weight	Expt. no.	% carbohydrate per wet weight
11	0·31	27	0·15
12	0·20	28	0·28
13	0·42	29	0·16
14	0·22	30	0·20
15	0·24	31	0·20
16	0·28	32	0·25
17	0·23	*33*a*	0·21
		*33*b*	0·24
18	0·22	34	0·17
19	0·25	35	0·27
20	0·20	36	0·20

* Expt. 33 was run in duplicate.

A certain amount of cannibalism had been suspected in some of the earlier pairs of fed and unfed experiments, but only Expt. no. 33 gave clear proof. Lucas (1936) found *Hemimysis* carrying dead mysids and amphipods, and he observed that the prey was being masticated. Tattersall & Tattersall (1951) also claimed that mysids were partly carnivorous.

It may be suggested that in those experiments listed in Table 4, where the unfed mysids showed very little or no reduction in carbohydrate as compared with fed animals, the reserves of carbohydrate were maintained to some extent by some of the so-called unfed *Neomysis* feeding on their less active fellows.

Attempts were made to limit cannibalism by reducing the starvation period (e.g. Expt. nos. 34–36: 4–5 h starvation), but this in turn raised difficulties in that the period was then likely to be insufficient to reduce carbohydrate reserves markedly. The short-term starvation results, in fact, fell well within the range for the whole unfed series—0·27 and 0·20%—and were by no means the lowest values obtained. While, therefore, it is difficult to ensure complete starvation conditions experimentally for *Neomysis*, there is little doubt that where marked reduction in feeding occurred, carbohydrate content was lowered.

The water content was determined on two samples of *Neomysis*, and the dry weight was found to be 19·0 and 19·9%, respectively, of the wet weight. As an approximation, therefore, the dry weight was reckoned as 20% of the wet weight, and the percentage of carbohydrate to dry body weight has been calculated for all the experiments. For fed animals the values varied from 2·10 to 1·00% (mean 1·30%); for unfed mysids, from 1·40 to 0·75% (mean 1·06%) (Tables 2 and 3).

Pleurobrachia pileus

The carbohydrate values found in *Pleurobrachia* varied from a maximum of 0·05% of the body (wet) weight to as little as 0·001%. In two experiments (Expt. nos. 42 and 50) the value was below 0·001%, though the precise level was uncertain. The very low values are explainable largely on the high water-content characteristic of ctenophores. The minimal values were barely detectable by the spectrophotometric method used, but the use of greater quantities of *Pleurobrachia* was not advantageous, since this also increased the volume of fluid. Although the figures for the lowest concentrations may be open to some criticism, there is no doubt that they are of the correct order of magnitude, and it therefore appears that there is an unusually wide range in the carbohydrate values obtained. This is in contrast to the results for both *Calanus* and *Neomysis*, where although a range was experienced, this was not nearly so great, unless animals were specifically starved. All the results quoted for *Pleurobrachia* in Table 5 were for fresh animals analysed as soon as possible—certainly the same day as collected. However, some hours elapsed, with the sorting of plankton hauls and preparation of the material, before the analyses, and this was especially true where several sets of determinations were made in one day. It is well known that *Pleurobrachia* is an active swimmer, and also a voracious and destructive carnivore, feeding on zooplankton. It is probable that like many other marine carnivores, the speed of digestion and assimilation is high, and the great variability in the carbohydrate content of freshly caught animals may reflect the variation between those that have fed very recently and those animals which have not eaten for a few hours. Some support for this theory comes from the analyses in Expt. nos. 58–62 (Table 5) which were specifically carried out on *Pleurobrachia* which were caught, sorted and used as rapidly as possible. The results gave carbohydrate contents varying from 0·010–0·007 %, i.e. the range was not so great, and no extraordinarily low values were obtained. By contrast, a few *Pleurobrachia* were left to starve in the laboratory in breffits of filtered sea water for 48 h. They were still healthy and active after starvation, but when analysed gave very much lower sugar values (viz. 0·0015–0·0010 %).

TABLE 5. CARBOHYDRATE CONTENT OF *PLEUROBRACHIA PILEUS*

Expt. no.	% carbohydrate per wet weight	% carbohydrate per dry weight
37	0·011	0·275
38	0·057	1·425
39	0·002	0·050
40	0·007	0·175
41	0·005	0·125
42	<0·001	<0·025
43	0·006	0·150
44	0·001	0·025
45	0·009	0·225
46	0·007	0·175
47	0·001	0·025
48	0·001	0·025
49	0·001	0·025
50	<0·001	<0·025
51	0·046	1·150
52	0·003	0·075
53	0·004	0·100
54	0·002	0·050
55	0·003	0·075
56	0·001	0·025
57	0·002	0·050
58	0·007	0·175
59	0·006	0·150
60	0·009	0·225
61	0·008	0·200
62	0·009	0·225

Expt. nos. 58–62 refer to determinations made on animals immediately following capture.

Though the evidence is not strong, these last experiments suggest that carbohydrate is utilized by *Pleurobrachia* fairly rapidly. Some *Pleurobrachia* were fed on zooplankton in the laboratory, but we were unable to feed a sufficient number to obtain a reliable analysis for experimentally fed animals. Analyses made by one of us (S. K.) on *Pleurobrachia* suggested that the dry weight of the body amounted to only 3·75 and 4·62 %, respectively, of the wet weight. This agrees fairly well with the values of 4·6 % (Cooper, 1939), and 4·5 % (Vinogradov, 1953). We have assumed a mean value of 4 % for all our experimental animals and from this we have calculated the percentage of carbohydrate to dry weight of body. The maximum obtained is 1·43 %, but values as low as 0·025 % were also found (Table 5).

DISCUSSION

The data presented on the carbohydrate reserves of certain planktonic animals, though preliminary, suggest that the amount of sugar in the body is low. For *Calanus* the maximum would appear to be of the order of 0·2% of the wet body weight; for *Neomysis*, where our values are a little more certain, the maximum is approximately 0·4% of the wet body weight It is of some interest that in a determination made on the copepod *Anomalocera patersoni* the amount of carbohydrate was 0·17% of the wet body weight. This is of the same order as the mean figure for freshly caught *Calanus*. For *Pleurobrachia*, as would be expected from the very high water content, even the maximum percentage (0·057%) is much lower than for the crustaceans, but the difference is less obvious if we calculate carbohydrate as a percentage of dry body weight. Thus, for *Neomysis* the maximum is 2·1%, whereas for *Pleurobrachia* it is 1·4%. These values are very much lower than those suggested by Brandt (1898) and Brandt & Raben (1919) for plankton. For example, for 'copepods', Brandt (1898) gives a summary: protein 59%, fat 7%, carbohydrate 20%, chitin 4·7%, ash 9·3%. Thus his figure for the amount of carbohydrate reckoned on a dry-weight basis is approximately × 10 our suggested values. However, Brandt's values are based on a few analyses of mixed marine plankton hauls (predominantly copepods) and also on some analyses of freshwater copepods, and it is difficult to compare his data with analyses of single species of zooplankton. It may be significant that Brandt & Raben (1919) give an analysis for a named zooplanktonic species (*Sagitta*) and the percentage of carbohydrate is then lower (*ca.* 14%).

Our preliminary data also suggest that there is a rise in carbohydrate in our animals with feeding. This agrees with the findings of previous workers, who showed a rise in blood sugar levels with feeding in crayfish and insects (Hemmingsen, 1924). There also appears to be a fall in the total carbohydrate content in starving planktonic animals, as has been found in the shore form *Carcinus* by Kleinholz & Little (1949), and this fall could be associated with activity, suggesting thus that sugars may be metabolized to some extent. However, as the rate of utilization of sugar is not rapid, it might be inferred that fat is utilized to a greater extent.

A few preliminary analyses of the fat content of *Neomysis integer*, using the method of Kumagawa & Suto (1908), as modified by von Brand, Weinstein, Mehlman & Weinbach (1952), gave fat values varying from 0·2 to 0·8% of the wet body weight. Since the dry weight is only a fifth of the wet weight of the body (p. 244) the amount of fat varies from 1 to 4% of dry body weight. Orr (1934*a*, *b*) quotes values of 20–40% as the fat content in *Calanus* and *Euchaeta*, reckoned on a dry-weight basis. Brandt (1898), however, gave a value of *ca.* 7% for copepods which is more comparable to the present figures.

It is generally known that carbohydrates may be converted into fats by many vertebrates. Whether a similar process is involved in these planktonic animals is uncertain, but it could be responsible for the low carbohydrate, as compared with high fat values, in zooplankton. It is also of interest to recall the suggestion made by Zeuthen (1955), based on respiratory quotient studies in butterflies, that carbohydrates, when they are metabolized, are first converted to fat before combustion in the muscles. Whether a similar process goes on in crustaceans is not known.

We are grateful to the Director and Staff of the Marine Biological Laboratory for all facilities during our work at Plymouth.

SUMMARY

The carbohydrate content of three species of planktonic animals (*Calanus finmarchicus*, *Neomysis integer*, *Pleurobrachia pileus*) was estimated.

In *Calanus* fed on phytoplankton the carbohydrate content varied from 2·24 to 0·63 μg per copepod or 0·18–0·05 % of the wet body weight. In fed *Neomysis* the carbohydrate content was 0·42–0·20 % of the wet body weight. Analyses of *Pleurobrachia* gave values for carbohydrate of 0·05–0·001 % wet body weight.

In all three species it appeared that starvation tended to lower the carbohydrate content.

The mean percentage of carbohydrate expressed as dry body weight is approximately 0·4 % for *Calanus*, 1·3 % for *Neomysis* and 0·2 % for *Pleurobrachia*.

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THE FECUNDITY OF ENGLISH CHANNEL PLAICE

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(Text-figs. 1–2)

This paper is the fourth in a series dealing with the fecundity of flatfish (Bagenal 1957*a*, *b*, 1958), and is concerned with the egg numbers in ripening female plaice *Pleuronectes platessa* L. caught in the English Channel.

On 27 November 1957, eighty-five plaice with maturing ovaries were caught in Rye Bay, Sussex; on 1 December, eight similar fish were caught in Lyme Bay, and during December sixty-four locally caught female plaice were brought in to the Plymouth Laboratory. The dates of the collections were chosen because in January 1957 I had found that a small proportion of the Plymouth plaice were spent. All the fish caught in November and December were at a suitable stage for fecundity estimation: that is, the eggs were well developed though none had begun to turn translucent.

The treatment of the fish was similar to that already described (Bagenal, 1957*a*) for long rough dabs, except that the Rye Bay and Lyme Bay plaice were weighed on a spring balance to the nearest quarter ounce and these weights were subsequently transformed to grammes; the Plymouth fish were weighed to the nearest 5 g. The paper on long rough dabs should be consulted for details of the laboratory methods of preservation, the estimation of the fecundity and the statistical analysis of the data.

I would like to thank Captain C. A. Hoodless and the crew of R.V. 'Sarsia' for their help at sea and Mr A. D. Mattacola and the Plymouth Laboratory staff for their help on land and also Miss Sheila Morris who counted the eggs.

RESULTS

The data are summarized in Tables 1 and 2 along with the fecundity data for the Clyde (from Bagenal, 1958) and for the Southern Bight of the North Sea (from Simpson, 1951). The relations of fish length and fecundity are shown in Figs. 1 and 2. The relations of age and fecundity are given in Table 3.

Plymouth

The fecundity of the Plymouth female plaice is the same as that of the Clyde fish; the difference between the two values for the expected fecundity ($\hat{F}$) of a 37 cm plaice could easily be due to random subsampling errors.

Simpson (1957) has found the fecundity of plaice from the Irish Sea to be similar to Clyde and Plymouth fish. The nearest locality from which he determined the fecundity was Cardigan Bay. It would be interesting to know the fecundity of the plaice that spawn off St Ives.

Plaice seem to be rare off Plymouth until mid-December at which time they begin to appear in increasing numbers prior to spawning in early January. We do not know where they come from.

TABLE 1. SUMMARY OF PLAICE FECUNDITY DATA

	Clyde	Plymouth	Lyme Bay	Rye Bay	North Sea
Number of fish	61	64	8	85	223
Mean length (cm)	38·33	42·47	37·57	38·35	37·13
Mean weight (g.)	585·8	758·8	688·1	518·8	518·4
Mean age	5·2	6·3	5·0	6·4	7·3
Mean fecundity	158,845	212,769	255,888	139,127	84,928
$\hat{W}$ for 37 cm	526·4	516·4	661·4	470·97	517·27
$\hat{F}$ for 37 cm	137,266	137,470	244,311	127,093	84,019

TABLE 2. THE MEAN FECUNDITY (IN THOUSANDS) OF EACH 3 CM LENGTH GROUP OF ENGLISH CHANNEL FEMALE PLAICE

Length group	Plymouth		Lyme Bay		Rye Bay	
	Number	Fecundity	Number	Fecundity	Number	Fecundity
30	—	—	—	—	6	70·21
33	5	125·06	4	172·80	23	89·62
36	8	113·88	2	131·20	16	117·82
39	10	129·62	—	—	14	125·83
42	13	207·71	1	324·95	12	186·60
45	14	247·20	—	—	6	173·25
48	8	266·62	—	—	2	250·60
51	3	313·82	—	—	2	268·53
54	2	419·85	—	—	1	230·35
57	—	—	1	768·55	1	264·15
60	1	709·55	—	—	—	—
63	—	—	—	—	2	442·63

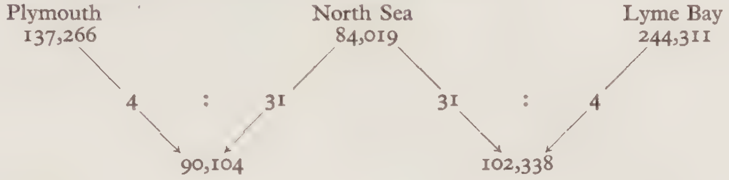
Rye Bay

The fecundity of the eighty-five Rye Bay plaice is intermediate between that of Plymouth and North Sea fish. From marking experiments in Rye Bay (Wimpenny, 1953) we know that the plaice migrate both into the North Sea and to the west. Wimpenny's results are summarized below.

Released	No.	Local returns	Eastward movement	Westward movement
January	300	56	31	4
April	?	87	49+	—
July	No tendency to move to the westward			
October	Suggested that what little movement there had been was in a westerly direction			

Three of the four westerly moving plaice were caught off Brixham (West end of Lyme Bay) and one from off South Ireland. Mixtures of west channel and

North Sea plaice in the ratio of 4:31 should produce a mean fecundity for 37 cm fish of between 90 and 102 thousand eggs.



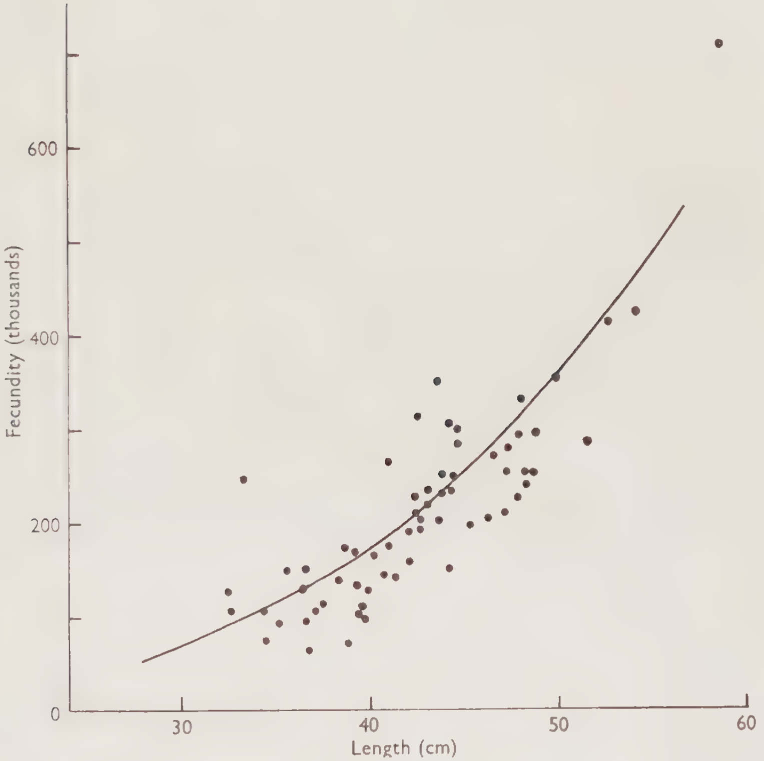


Fig. 1. Scatter diagram showing the relation of fecundity and length of plaice from Plymouth and the calculated curve for Clyde fish (Bagenal, 1958).

The actual fecundity of 127 thousand eggs for 37 cm plaice might be the average of fish mainly derived from the North Sea, but with a mixture of more plaice from the west than marking experiments suggest do exist in the area: over one-third of the population would have to be of western origin. Moreover, the scatter diagram (Fig. 2) shows that the general level of fecundity for the Rye Bay population as a whole is above that of the North Sea.

Simpson (1959) discusses the spawning of North Sea plaice and believes that 'the spawning area in the eastern English Channel is not an independent spawning area, but is, in effect, a spill-over from the main Southern Bight area'. If this is true either the spill-over is not of typical North Sea fish but selects the more fecund, or having arrived in the area the conditions are such (more food, etc.) as to allow them to produce more ova. Another hypothesis would be that the eastern Channel plaice form a separate stock with a characteristically higher fecundity (perhaps due to crossing with west channel

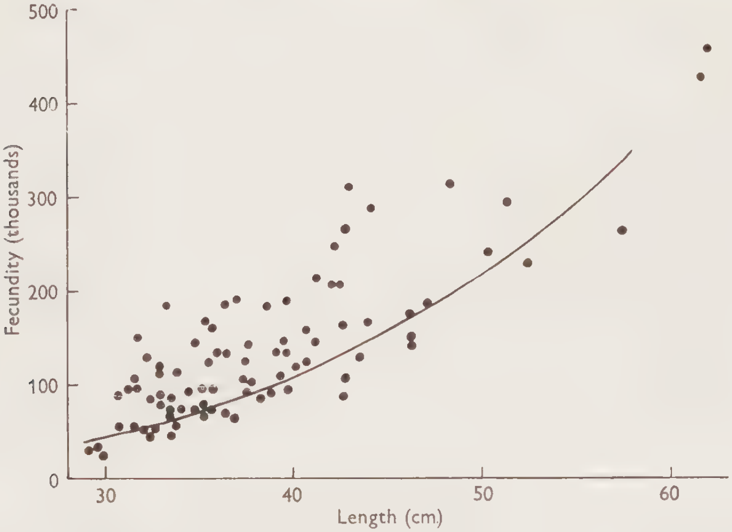


Fig. 2. Scatter diagram showing the relation of fecundity and length of plaice from Rye Bay and the calculated curve for fish from the Southern Bight of the North Sea (Simpson, 1951).

TABLE 3. THE MEAN FECUNDITY AND LENGTH OF EACH AGE GROUP OF FEMALE PLAICE CAUGHT IN THE ENGLISH CHANNEL

	Plymouth			Lyme Bay			Rye Bay		
Age group	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity
II	—	—	—	—	—	—	4	31·3	96·4
III	4	36·2	162·1	2	32·7	242·6	10	32·9	77·6
IV	4	38·6	164·9	1	36·2	158·8	9	34·9	124·3
V	15	40·6	172·8	3	33·1	103·2	16	34·6	107·8
VI	11	42·3	198·6	1	41·8	325·0	13	37·6	124·0
VII	12	41·5	183·6	—	—	—	9	37·0	122·9
VIII	6	46·9	298·5	—	—	—	4	42·7	221·1
IX	6	46·6	239·3	1	57·9	768·6	8	43·3	139·3
X	2	53·4	419·9	—	—	—	3	43·7	154·0
XI	—	—	—	—	—	—	2	44·5	206·0
XII	—	—	—	—	—	—	2	46·7	277·1
XIII	—	—	—	—	—	—	—	—	—
XIV	—	—	—	—	—	—	1	52·5	230·4
XV	—	—	—	—	—	—	1	57·5	264·2
XVI	—	—	—	—	—	—	1	51·3	296·6
XVII	—	—	—	—	—	—	1	61·7	427·9

fish). This would involve the return of those adult fish that migrate into the North Sea as well as the return of the young that have drifted there as eggs and larvae The return of young to the exact breeding place of their parents is well known in salmonids and birds.

The growth rate of eighty-five Rye Bay plaice as shown in Table 3 is comparable to that given by Wimpenny (1947) after allowance is made for the time of year of the collections. The rate of growth is faster than that of North Sea plaice, and this is similar to the situation at Flamborough.

It is perhaps significant that the smaller areas such as Flamborough and Rye Bay that are out-lyers of the main North Sea plaice grounds carry stocks with higher fecundities, and faster growth rates.

Lyme Bay

The eight Lyme Bay plaice have a high mean fecundity but this is to some extent increased by one fish of 58 cm in length which was exceptionally fecund.

Four hours fishing off Brighton, and some 12 h trawling in Poole Bay did not yield any plaice and the eight females from Lyme Bay were caught in over 4 h fishing.

In the middle region of the Channel therefore plaice are very scarce in late November, and even at Plymouth they do not appear to become plentiful until mid-December. It is not possible at this stage to confirm an inverse relation between fecundity and population density, because of the complications imposed by migration. Nor is a relation between fecundity and condition immediately apparent. This is shown by the North Sea plaice which were in better condition than those in Rye Bay (a 37 cm fish has a heavier expected weight) but had a lower fecundity.

SUMMARY

The plaice off Plymouth are shown to have a level of fecundity comparable to the Irish Sea and Clyde. The plaice in Rye Bay have a fecundity intermediate between that of the Clyde–Irish Sea–Plymouth fish, and the North Sea plaice, but this is apparently not produced by a mixing of the two populations, either the environment favours a high fecundity, or the Eastern Channel plaice form a separate stock.

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THE FECUNDITY OF PLAICE FROM THE SOUTH AND WEST COASTS OF IRELAND

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(Text-figs. 1–3)

This paper is the fifth in a series dealing with the fecundity of flatfish (Bagenal, 1957*a*, *b*; 1958, 1960), and is concerned with the numbers of eggs in the roes of ripening female plaice *Pleuronectes platessa* L. caught off the south and west coasts of Ireland during November and December 1958. The fish were obtained from Wexford, Ballycotton, Schull, Dingle, Galway and Killybegs (Fig. 1).

The fish were bought immediately after being landed either direct from the fishermen, when the whole female catch was obtained, or through An Bord Iascaigh Mhara when a predetermined number were taken as they lay in a fish box. The fish bought from the fishermen were ungutted, but those obtained from the Board had been gutted. A few of the latter fish had to be rejected as the ovaries were damaged, but it was an insignificant percentage. Thereafter the treatment of the fish, storage of the ovaries, the subsampling and counting of the eggs and the statistical analysis of the results were all as described in an earlier paper (Bagenal, 1957*a*) except that the four aliquot samples of eggs consisted of 1/410 instead of 1/200. This greatly reduced the time and labour of egg counting.

I would like to thank the employees of An Bord Iascaigh Mhara who helped me in Ireland and Miss Sheila Morris for her help in the laboratory.

RESULTS

The data are summarized in Tables 1–3, and the relation of fish length and fecundity are shown in Figs. 2 and 3. The expected weight ($\hat{W}$) and the expected fecundity ($\hat{F}$) of a fish 37 cm long are also shown in Table 1. They were calculated from the regression equations of log length on log weight and on log fecundity, respectively, and may be used for comparing the different populations. The regression coefficients (*b*) are also shown. (For details of the calculations see Bagenal, 1957*a*.) Numerous tests were made to see if any of the differences in fecundity and condition were significant.

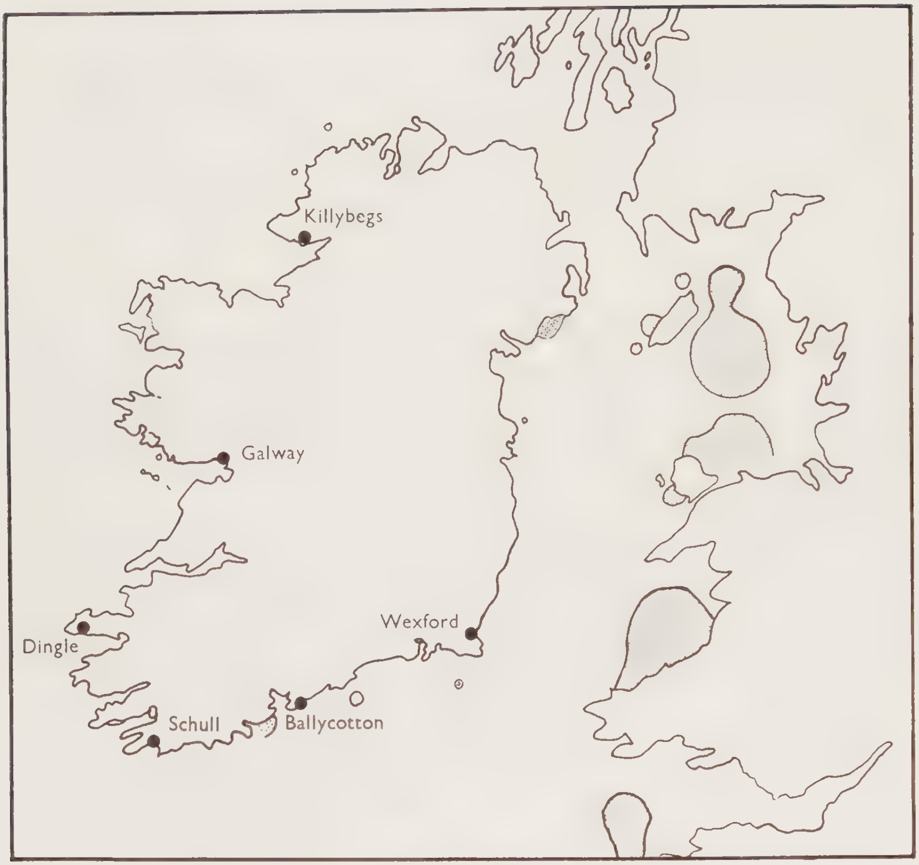

Fig. 1. Map of Ireland and the Irish Sea, showing localities from which plaice were collected, and (stippled) the spawning areas found by Simpson.

Wexford

Simpson (1959*b*) made a survey of plaice eggs in 1952 and 1953 in the Irish and Celtic Seas from Newcastle (Co. Down) to west of Cork. He gives maps indicating the occurrence of newly spawned eggs. The largest concentration of eggs nearest to Wexford was found in Cardigan Bay (about 60 miles to the east across St George's Channel on the Welsh coast), and, although one egg was found south of Saltee Island, the Wexford plaice probably belong to the Cardigan Bay stock. The fecundity of the Wexford plaice was not found to differ from that of the Plymouth plaice (Bagenal, 1960) or from those of the Clyde (Bagenal, 1958) and appear to be similar to those in the Irish Sea for which Simpson (1957) has given the preliminary results. The plaice on the north–south line through the Clyde–Irish Sea–West Channel on longitude 5° west have similar fecundities.

Ballycotton

Simpson found one planktonic plaice egg off Minehead in 1955 (Survey 1, 23 January–3 February). I found plaice very scarce at Ballycotton, 20 miles west. Their fecundity, however, was high.

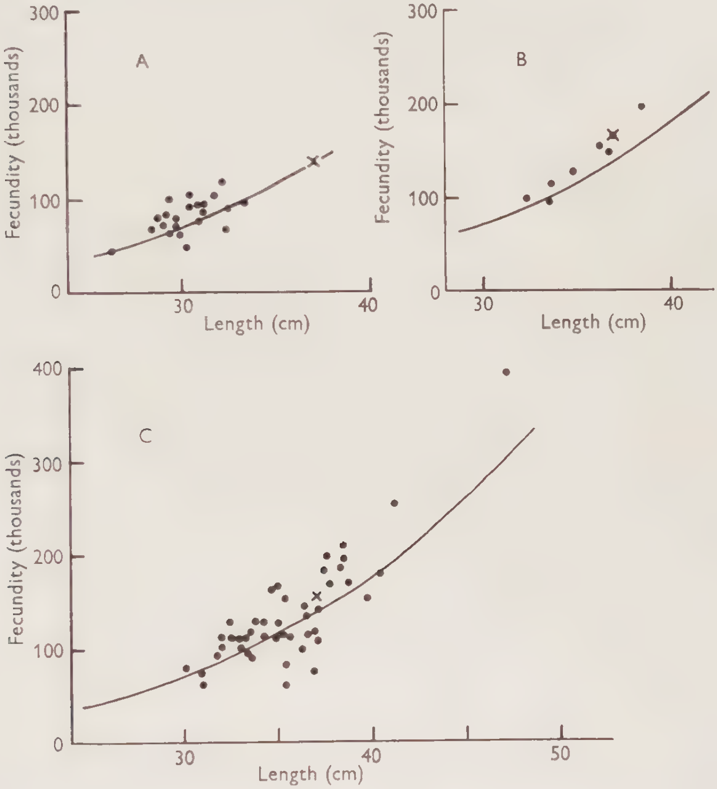

Fig. 2. Scatter diagrams showing the relation of fecundity and length of plaice from (A) Wexford, (B) Ballycotton and (C) Dingle. In some cases dots are superimposed on others. The expected fecundity ($\hat{F}$) of fish of 37 cm is shown in each diagram by × and the calculated curve for Clyde fish is given for comparison.

Schull

West of Cork Simpson appears to have found the edge of a concentration of plaice eggs whose centre lay farther still to the west. At Schull, plaice were again scarce and only ten could be got in a reasonable time. Even though the Schull and Ballycotton plaice have very high fecundities, they are not statistically significantly different from those of Wexford, but the samples are unfortunately very small.

Dingle

At Dingle, plaice were plentiful and the roes from a good sample of fifty fish were easily obtained. These, like those from Schull, have a high fecundity. Their fecundity is significantly higher than that of Plymouth fish (at the 5 % probability level) and the Clyde plaice (at the 1 % level) but is not statistically different from those of Wexford. There are only thirty fish to test them against at Wexford, compared with over sixty from both the Clyde and Plymouth.

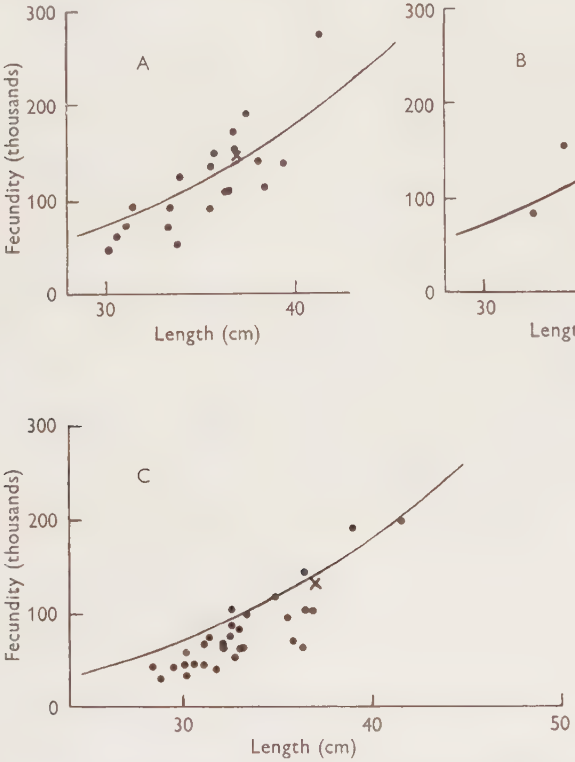

Fig. 3. Scatter diagrams showing the relation of fecundity and length of plaice from (A) Galway and (B) Schull and (C) Killybegs. In some cases dots are superimposed on others. The expected fecundity ($\hat{F}$) of fish of 37 cm is shown in each diagram by × and the calculated curve for Clyde plaice is given for comparison.

Galway

The Galway plaice were caught off Clare Island. Their fecundity is lower than that of the Dingle fish, but the difference is not statistically significant.

TABLE 1. SUMMARY OF IRISH PLAICE FECUNDITY DATA

	Wexford	Bally-cotton	Schull	Dingle	Galway	Killybegs
Number of fish	30	8	10	50	20	31
Mean length (cm)	30·67	35·40	37·59	35·51	35·41	33·17
Mean weight (gr)	292·63	458·50	549·90	483·56	464·70	358·52
Mean age (years)	2·9	3·3	2·8	3·1	3·2	3·8
Mean fecundity	84,002	139,336	158,137	133,195	120,811	82,162
W for 37 cm	505·3	539·2	523·8	549·4	521·4	501·2
F for 37 cm	139,612	169,342	150,641	152,775	146,182	132,120
Regression coefficient (*b*)	2·71	4·15	3·10	3·33	4·33	4·35

TABLE 2. THE MEAN FECUNDITY (IN THOUSANDS) OF EACH 3 CM LENGTH-GROUP OF IRISH FEMALE PLAICE

Length group	Wexford		Ballycotton		Schull	
	No.	Fecundity	No.	Fecundity	No.	Fecundity
27	1	45·72	—	—	—	—
30	21	81·39	—	—	—	—
33	8	95·63	3	104·76	2	116·65
36	—	—	4	150·42	4	146·19
39	—	—	1	198·75	2	140·48
42	—	—	—	—	2	241·18
45	—	—	—	—	—	—
48	—	—	—	—	—	—

Length group	Dingle		Galway		Killybegs	
	No.	Fecundity	No.	Fecundity	No.	Fecundity
27	—	—	—	—	—	—
30	3	70·42	3	60·92	9	47·83
33	17	107·77	5	87·74	13	78·21
36	19	122·98	7	132·11	7	101·08
39	8	181·57	4	148·04	1	192·60
42	2	216·17	1	277·88	1	199·67
45	—	—	—	—	—	—
48	1	394·83	—	—	—	—

TABLE 3. THE MEAN FECUNDITY AND LENGTH OF EACH AGE-GROUP OF FEMALE PLAICE CAUGHT OFF SOUTH AND WEST IRELAND

Age group	Wexford			Ballycotton			Schull		
	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity
II	6	31·4	103·6	—	—	—	3	35·8	115·8
III	21	30·4	79·5	4	34·0	117·5	5	38·9	178·5
IV	3	31·1	76·2	2	35·8	139·8	1	37·0	198·0
V	—	—	—	—	—	—	—	—	—
VI	—	—	—	—	—	—	—	—	—
VII	—	—	—	—	—	—	—	—	—
VIII	—	—	—	—	—	—	—	—	—

Age group	Dingle			Galway			Killybegs		
	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity	No.	Mean length	Mean fecundity
II	16	33·2	109·2	4	34·0	96·5	3	30·6	61·5
III	18	35·3	123·5	10	34·0	98·6	12	31·7	61·9
IV	10	37·4	156·7	4	38·9	196·7	9	34·0	93·3
V	1	40·5	178·2	2	38·4	129·0	3	33·4	68·8
VI	1	35·2	122·8	—	—	—	3	35·9	124·7
VII	—	—	—	—	—	—	1	41·6	119·7
VIII	1	47·3	394·8	—	—	—	—	—	—

Killybegs

Thirty-one female plaice were sampled at Killybegs, the fish having been caught in Donegal Bay. The fecundity is lower than at Galway, and significantly lower at the 1 % level than the fecundity of the Dingle fish, but the mean fecundity of the Killybegs plaice does not differ significantly from the Clyde fish, though the slopes of the lines ($b = 3 \cdot 21$ for the Clyde and 4·35 for Killybegs) are nearly significantly different at the 5 % level.

DISCUSSION

The fecundity of plaice increases westwards along the south coast to Dingle and then decreases northwards along the west coast to Killybegs. Added to these general trends there is a further feature that small populations of plaice which are living in 'bleak' habitats appear to have a higher fecundity than neighbouring larger populations. This is seen at Ballycotton and Schull, as well as at Lyme Bay (Bagenal, 1960). The mechanism behind these differences in fecundity is still obscure, but the survival value of them is quite clear. Dingle and Schull, being in the south-west of Ireland, are not only in an extremely exposed region, but also are in the track of the prevailing south-westerly winds and currents. There will therefore be a much greater chance of the planktonic eggs and young being transported long distances, than for example in the North Sea. Similarly, in small populations the dispersal of the planktonic eggs and larvae may at times be catastrophic. In both cases a high fecundity will increase the chances of sufficient of the progeny being able to return to the breeding area. This view implies that the fish return to the area where they themselves were spawned regardless of their movements in the meantime.

A similar explanation (Bagenal, 1960) has been put forward for the higher fecundities that have been found with Flamborough and Rye Bay plaice, both of which are small outliers of the main North Sea population. The North Sea plaice that spawn to the south of the Dogger Bank, and particularly the largest concentration in the Southern Bight (Simpson, 1959*a*, fig. 35), have the lowest fecundities that have been recorded for this species (Simpson, 1951), and this is a relatively sheltered and enclosed area.

A further point of significance is the ranked order of fecundity and condition. For the Irish data given in Table 1, the ranks are

Condition		Fecundity	
Dingle	549	Ballycotton	169
Ballycotton	539	Dingle	153
Schull	524	Schull	151
Galway	521	Galway	146
Wexford	505	Wexford	140
Killybegs	501	Killybegs	132

The ranked order for fecundity and condition of fish including data from other British areas is given below.

Condition		Fecundity	
Lyme Bay	661	Lyme Bay	244
Dingle	549	Ballycotton	169
Ballycotton	539	Dingle	153
Clyde	526	Schull	151
Schull	524	Galway	146
Galway	521	Wexford	140
North Sea	517	Plymouth	137·5
Plymouth	516	Clyde	137·3
Wexford	505	Killybegs	132
Killybegs	501	Rye Bay	127
Rye Bay	471	North Sea	84

The difference here, apart from the interchange of positions by Ballycotton and Dingle, and by Wexford and Plymouth, are due to Clyde and North Sea being four places higher in the fecundity rank. The most likely reason for the greater weight of these fish is that they were probably caught earlier in the year, that is, a longer time before the spawning season. As the time of spawning approaches the condition of the somatic tissue decreases very rapidly though the gonads of course are increasing in weight. It is for this reason that I attach little importance to the weight of the fish or their gonads in fecundity work (cf. Kändler, 1959), unless the spawning season is well known. That these weights are important factors to be considered if the spawning dates are known is obvious, and they may be useful when comparing two nearby localities at nearly the same time. In this case the fish will probably be at comparable stages in their breeding development. This, I think, is true of the Irish data.

Another point that is apparent from Table 3 is that the growth rate also increases along the south coast, and decreases again northwards. At Dingle the mean length of eighteen fish in the III age-group was 35·3 cm, though in the North Sea plaice often do not reach this length until their sixth year. The order of localities ranked for the rate of growth of fish is not the same as for condition or fecundity, though as has been found elsewhere (Simpson, 1951; Bagenal, 1958) the fast growing fish do tend to be those with the higher fecundity.

SUMMARY

The fecundity of plaice from six localities on the south and west coasts of Ireland has been analysed. For a 37 cm fish the fecundity increases from about 140 thousand eggs at Wexford to 153 thousand eggs at Dingle, and decreases northwards to 132 thousand at Killybegs, though at Ballycotton and Schull where plaice are scarce the fecundity is unusually high. It is suggested that the fecundity is an adaptive character, being highest in the poorer habitats and in regions where the dispersal of the planktonic stages will be greatest. This

implies that plaice, like other fish, return to an hereditary spawning area. In the poor habitats the fish have to be in good condition, grow fast and have a high fecundity in order to survive.

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THE MOTILE (*CRYSTALLOLITHUS HYALINUS* GAARDER & MARKALI) AND NON-MOTILE PHASES IN THE LIFE HISTORY OF *COCCOLITHUS PELAGICUS* (WALLICH) SCHILLER

By Mary Parke and Irene Adams
The Plymouth Laboratory

(With 43 Figures on Plates I–IV)

A new coccolithophorid, *Crystallolithus hyalinus*, was described with the help of electron micrographs by Gaarder & Markali in 1956 from preserved material in which the cells lacked the appendages. From temporary cultures set up from our September 1957 sea-water samples a coccolithophorid was isolated which appeared, under the light microscope, very similar to this newly described coccolithophorid but which possessed, as does the genus *Chrysochromulina*, a coiling haptonema in addition to the two flagella. Electron micrographs, taken for us by Prof. I. Manton, have shown that the holococcoliths from our organism are identical in structure with those from the *Crystallolithus hyalinus* (cf. Pl. I, and Gaarder & Markali, 1956, pl. I).

In addition, we have shown by culturing that the motile *C. hyalinus* bearing holococcoliths (crystalloliths) is in fact the motile phase in the life history of another coccolithophorid previously known only in the non-motile phase. This non-motile phase, bearing heterococcoliths (placoliths) which are structurally different from those borne on the motile phase, can be referred to the well-known species *Coccolithus pelagicus* (Wallich) Schiller.

The finding of two distinct structural types of coccoliths (see Braarud, Deflandre, Halldal & Kamptner, 1955; Halldal & Markali, 1955; Kamptner, 1958) in the life history of one coccolithophorid will necessitate a complete reassessment of the problems connected with the classification of the Coccolithophoridae.

Very grateful thanks are due to Prof. Irene Manton for examining our organism under the electron microscope and for compiling for us Plate I of this paper. We are also indebted to Dr L. H. N. Cooper and Mr E. I. Butler for the collection of sea-water samples, and to Mrs B. Hepper for testing this organism for its possible toxicity to fish.

THE MOTILE 'CRYSTALLOLITHUS' PHASE

As two strains (Plymouth no. 182, at position 50° 02′ N., 04° 22′ W., at 10 m on 17 September 1957, deposited with the Collection of Algae and Protozoa, Cambridge; Plymouth no. 217, at position 47° 19′ N., 07° 23′ W., at 20 m on 20 April 1958) are being maintained in the Plymouth culture collection, additional information from living material can be given to supplement the description given by Gaardner & Markali from preserved material.

The Crystallolithus phase swims only for short periods in one direction and moves comparatively slowly, rotating slowly also but showing sometimes considerable gyration. It can swim with the flagella and haptonema in front, or behind the body with the haptonema coiled or extended. As in some *Chrysochromulina* species (Parke, Manton & Clarke, 1955, 1956) swimming is more rapid when the flagella and haptonema are directed backwards, but unlike most of the *Chrysochromulina* species in which the haptonema is coiled during rapid swimming, the haptonema in this form is seen more usually fully extended when swimming in either direction.

In culture the cells of this phase are globose to subglobose, measuring 8–18 (exceptionally 6–20) μ in diameter (in a rapidly growing culture 18 % of the cells are 6–10 μ, 55 % 10–15 μ, and 27 % 15–20 μ). The uninucleate cells have two or four deep golden brown parietal saucer-shaped to oblong chromatophores, deeply cleft into two at the non-flagellar pole. Conspicuous lipid bodies lie near the inner faces of the chromatophores, and leucosin vesicles are developed towards the non-flagellar pole. Two acronematic flagella, usually homodynamic, and one haptonema arise close together at one pole (Pls. I, II). The flagella are very fine and rather stiff, equal or unequal in length, 1·5–2·5 times the cell diameter in length. There can be a difference of up to 6 μ in the length of the two flagella of an individual cell. The short haptonema, thinner than the flagella and coiled round once or twice when not extended as a rod, usually measures $\frac{1}{2}$ to $\frac{3}{4}$ of the cell diameter in length when fully extended; it has a small club-shaped tip and shows a basal swelling (Fig. 2, Pl. I) similar to that found in *Chrysochromulina kappa* (Parke *et al.*, 1955, pl. IV) and *C. ericina* (1956, pl. II).

The periplast of the cell has embedded, in its surface layer, very thin transparent oval to elliptical sculptured plate-scales, the sculpturing being visible only with the electron microscope. The scales show on one face a radiating pattern of ridges which reach to the edge (Fig. 4, Pl. I), while the other face usually shows either a network of fibres (Fig. 5, Pl. I) or sometimes roughly concentric surface ridges of varying width. In any one cell the scale size can range from 0·4 to 3·3 μ in diameter but the most frequent size is from 1·5 to 2·0 μ.

The Crystallolithus phase of *Coccolithus pelagicus* differs from the motile phases of members of the genus *Chrysochromulina* in having calcite microcrystals deposited on the scales, and also apparently in the composition of the periplast. In addition to showing that scale size is extremely variable the electron micrographs have shown also that the calcite microcrystals, deposited on the scales in a definite pattern, the 'holococcolith' or 'crystallolith' (Braarud *et al.*, 1955), vary considerably in size depending on scale size. Scales below 1 μ show no crystals, but scales about 1 μ in length show a deposit of microcrystals which are clearly distinguishable (see centre Fig. 3, Pl. I). The edge length of the microcrystals can vary from 430 to 2500 Å according to the size of the scale.

In the Crystallolithus phase the body has a two-layered covering, an inner distinct layer, which is clearly visible in Figs. 13–16, Pl. II, and an outer hyaline striated layer in which the scales, bearing the crystalloliths on their outer face, are embedded (Figs. 8–16, Pl. II). With Schultze's solution the inner layer gave a reaction suggesting cellulose, but the outer hyaline layer failed to give any reaction for pectic material with Ruthenian Red; its composition therefore is unknown. This outer hyaline layer varies very considerably in thickness in different individuals, the range of thickness being from apparently absent (Fig. 7, Pl. II) to being about 2·5 μ thick (Figs. 8–16, Pl. II). The change in thickness of this outer layer will be dealt with in the section on reproduction.

Frequently more than one layer of crystalloliths can be distinguished in this outer striated layer (Figs. 11, 13, 16, Pl. II) but in spite of these layers of material surrounding the body, the Crystallolithus phase can exhibit phagotrophy as do the marine species of *Chrysochromulina* that have been studied (Parke *et al.*, 1955, 1956, 1958, 1959). Phagotrophy occurs very frequently, the cells ingesting graphite, bacteria and plant cells up to a size of 5 μ (Figs. 27, 28, Pl. III). Ingested material is taken in at the non-flagellar pole and is digested usually in the region towards that pole. An unusual procedure for the discarding of waste material then occurs which has not previously been recorded, although the discarding of empty walls of plant cells through a tube was reported for *Chrysochromulina ericina* (Parke *et al.*, 1956, p. 398). In the Crystallolithus phase waste material, still in active Brownian movement, is passed out of the body into the outer hyaline layer where it collects in a globule (or vacuole) which is pushed out gradually from the hyaline layer, taking part of this layer with it including the crystalloliths. It is then cut off from the cell surface and discarded as a sack or sphere. This process takes place more usually near the non-flagellar pole, but it has been seen to occur near the flagellar pole. The discarded globules can measure up to 7·5 μ in diameter. Under dark field it can be seen clearly that they are covered by coccoliths, and filled with minute granules still in active Brownian movement, but in preserved material these discarded globules could quite easily be mistaken for small coccolithophorids. The Crystallolithus stage has been tested and found non-toxic to fish.

Reproduction of the motile Crystallolithus phase is by fission to produce generally two daughter-cells of equal or unequal size. Incipient fission stages (Fig. 15, Pl. II) measure 18–21 μ in diameter but double fission stages producing more usually three daughter-cells but occasionally four and measuring 28–30 μ in diameter are not uncommon (cf. *Chrysochromulina*, Parke *et al.*, 1955, figs. 11, 44, 70). In the incipient fission stages the outer hyaline layer containing the crystalloliths has reached its maximum thickness and during fission appears to swell up and become detached from the body surface so that the two daughter-cells when they have rounded off lie free inside it. The daughter-cells emerge from this outer layer leaving it behind as an empty case (Fig. 31, Pl. IV) and in cultures the bottom of the flasks have a thick covering of these empty cases which persist for a considerable time. In the newly liberated daughter-cells (Fig. 7, Pl. II) the hyaline layer cannot be detected although both it and the sculptured scales may be present. The crystalloliths are definitely not developed at this stage but as the daughter-cell secretes a new hyaline covering, apparently in concentric layers, the crystalloliths are gradually produced on the scales (Figs. 8–14, Pl. II). Although the usual procedure is for the daughter-cells to emerge from the outer clear layer as 'naked' stages it is not unusual for the outer hyaline layer of the mother-cell, or part of it, to remain attached to the outside of the daughter cells so that when the new hyaline layer of the daughter-cell containing the crystalloliths is laid down, there is a second outer layer containing crystalloliths covering part of, or the whole of, the cell (Fig. 13, Pl. II).

THE NON-MOTILE *COCCOLITHUS PELAGICUS* PHASE

The stages in the life history found so far suggest very strongly a type of life history similar to that found in the *Chrysochromulina* species that have been studied (cf. Parke *et al.*, 1955, p. 593). The motile Crystallolithus cells pass into the non-motile phase when a culture is 5–8 weeks old. The cells collect on the bottom of the flask as a dark olive brown skin, which, if examined soon after its formation, shows masses of Crystallolithus-sized cells, the majority of which still retain the outer hyaline layer containing the crystalloliths (Fig. 16, Pl. II; Figs. 19, 29, Pl. III). At this early stage the cells, although lacking flagella, appear to retain their haptonemata as organs of attachment, as do the cells of the coccolithophorid, *Pleurochrysis scherffelii* Pringsheim, during the early stages of the non-motile phase. If samples of this skin from a Crystallolithus culture are not examined until about 2 weeks after its formation then the non-motile stages illustrated on Pl. III can usually be found. Among the smaller non-motile Crystallolithus individuals (Fig. 19), cells of much larger size (25–60 μ) have developed (Figs. 20–26) but their origin has not so far been traced. Fusion stages have been looked for consistently in cultures in this stage, but without success. Although knowledge of the first stage in the production of the large cells is lacking (cf. *Chrysochromulina*, Parke *et al.*, 1955, p. 593), unless it is just a type of cyst formation in which there is a gradual increase in cell size, the later stages in their development have been recorded. Whether or not the initial stage in the production of the large cells is a fusion of two cells there is still further enlargement during the later stages of development.

In the earlier stages of enlargement the cells (25–35 μ), still surrounded by the hyaline layer (Fig. 20), develop very large leucosin vesicles, which can fill up to three quarters of the volume of the cell (Figs. 20, 21). Later stages show either four (Fig. 30) or eight disk-shaped chromatophores (Fig. 22) and leucosin vesicles usually of smaller size. With further increase in cell size (35–60 μ) the leucosin reserve disappears (Fig. 20, bottom cell), the chromatophores become more lobed (Fig. 23) and numerous spheroidal to ovoid vesicles (2·5–5·5 μ), which darken on the outside with osmium tetroxide, gradually develop in the cells (Figs. 24–26). The production of these vesicles is an indication that the large placoliths of the *Coccolithus pelagicus* phase are beginning to form inside the cell. Single placoliths have been seen inside these large cells which still retain a very thin outer hyaline layer round the body (Fig. 26).

Normally the placoliths are deposited on the cell surface inside the thin hyaline layer (Fig. 17, Pl. II) before the double division of the large *C. pelagicus* mother-cell (Figs. 32, 36) to produce four *C. pelagicus* daughter-cells (Figs. 38–40, 42, 43); nevertheless, fission of the mother-cell into two (Fig. 25, Pl. III) or four (Fig. 26, Pl. III) can start while the placoliths are being deposited on the body surface. Our measurements of the different stages indicate that the mother-cells contract considerably in size while the placoliths are being deposited on the body surface (cf. similar stage in *Chrysochromulina* species, 1955, p. 593).

In culture, both the *Coccolithus pelagicus* mother- and daughter-cells show a wide range in size. The mother-cells are usually ovoid (Figs. 32, 36), measure from 25 to 40 μ in diameter, and bear from 25 to 35 placoliths, while the daughter-cells are always spheroidal in shape, measure from 10 to 22·5 μ in diameter, and bear from 8 to 17 placoliths. Sometimes the two *C. pelagicus* cells, product of the first division of the mother-cell (Figs. 38, 39), separate before the second fission; their size is from 20 to 30 μ and they bear from 16 to 28 placoliths. The placoliths on all stages are generally ovate in surface view (Fig. 33) with a central oval pore, usually subdivided by a bar into two equal parts (Fig. 6, Pl. I; Fig. 33, Pl. IV), but it is not uncommon for the dividing bar to be lacking; they measure usually from 8 to 11 μ in length but lengths of from 4·4 to 13 μ have been recorded. Placoliths circular in surface view, with a single central round pore, have also been observed, usually on daughter-cells, and placoliths abnormal in shape are also occasionally produced (Fig. 37). Thus, from the measurements obtained from culture the range of size of *C. pelagicus* cells that might be found in the sea is from 10 to 40 μ with the cells bearing from 8 to 35 placoliths, the placoliths themselves varying from 4·4 to 13 μ in length.

Although the natural emergence of a Crystallolithus motile cell from a *C. pelagicus* daughter-cell has not been witnessed, it is possible to force out the Crystallolithus cell from its covering by exerting slight pressure on a daughter-cell ready to liberate its contents. The cell which emerges has two chromatophores and is similar in appearance to the Crystallolithus cell illustrated in Fig. 7, Pl. II, except that the flagella and haptonema are lacking. Cells released in this way have a diameter 3–5 μ less than that of the placolith covering. Normal release is by a pore produced by the casting off of a single placolith (Fig. 41, Pl. IV), which can be seen frequently still attached by one edge to the empty daughter-cell.

Cultures of this organism have been started each month throughout the year by inoculating with the motile phase. In the spring, the *C. pelagicus* phase can occasionally be found in cultures 5–7 weeks old, but at other times of the year the cultures are more usually 10–12 weeks old, sometimes older, before the *C. pelagicus* phase is produced. *C. pelagicus* can persist in unialgal culture in a healthy condition for at least 12 months (records for longer period not yet available) without being subcultured and without the addition of nutrients other than those in the medium (Erd-Schreiber) when the culture was started. Our records for the 12-month period, for a number of cultures, show that there is a regular alternation of the motile Crystallolithus and the non-motile *C. pelagicus* phase during the period. The persistence in unialgal culture of this species for such a long period in a healthy and vigorous state, without requiring additional nutrients (including iron) for rapid growth, suggests that the phagotrophy shown by the motile Crystallolithus phase may be in part responsible for this behaviour.

For the years 1921–22, Lebour (1923) records *C. pelagicus* (non-motile phase) as occurring at all depths from the surface to 100 m almost all the year round from the Plymouth region, the western part of the Channel and outwards towards the Irish Sea and the French coast. It was most frequent in March and October and less frequent from June to August than in the remaining months. Our records, for the nanoplankton occurring at Stations E1 and L2 to 6 for 1957–59, show that this phase occurs now much less commonly in the waters off Plymouth than it did in 1921 and 1922. In the three years 1957-59 its presence was recorded during three periods only, September 1957 to January 1958 (frequent, surface to 70 m), February and March 1959 (rare, surface to 20 m), and October to December 1959 (frequent, surface to 70 m).

The Crystallolithus phase, however, was recorded five times during the same period from the following stations and depths: E1, 17. ix. 57, 10 m with *C. pelagicus* phase; L6, 15. x. 57, surface, with *C. pelagicus* phase; L5,

9. vii. 58, surface; L4, 9. vii. 58, surface; E1, 26. viii. 58, surface. It has also been recorded from the southern Celtic Sea and the north-eastern Bay of Biscay in slope and oceanic water during March and April 1958, at a depth of 10–20 m but at no other depth. In March, the *C. pelagicus* phase was also present at 20 m in the oceanic water.

Recent records for the occurrence and distribution of the Crystallolithus and *C. pelagicus* phases can be found in Braarud, Gaarder & Grøntved (1953), Gaarder & Markali (1956), Smayda (1958), and for the *C. pelagicus* phase only, in Bernard (1942), Lecal-Schlauder (1951), Halldal (1953), and Gaarder (1954). For the Norwegian Sea in May 1948, Braarud, Gaarder & Grøntved (1953) record the Crystallolithus phase as reaching a maximum density of 17,500 cells l. at the surface and the *C. pelagicus* phase as reaching a maximum density of 20,000 cells/l. at 50 m.

DISCUSSION

We have called this organism by the name in current usage (Schiller, 1930; Lecal-Schlauder, 1951; Kamptner, 1954), *C. pelagicus* (Wallich) Schiller, and Mrs Karen Ringdal Gaarder has confirmed (private communication) that this name is the legitimate name for this organism.

When Gaarder & Markali (1956) described *Crystallolithus hyalinus* they suggested it might be identical with *Pontosphaera borealis* Ostenfeld (1910), described from arctic water of the East-Greenland Sea, but they were doubtful because coccoliths 3–4 μ long were recorded for *P. borealis*, while their preserved material of *Crystallolithus* had coccoliths only 2 μ long. We have shown earlier that the coccoliths on the Crystallolithus phase can be up to 3·3 μ long, and, as further supporting evidence of the two motile forms being identical, Ostenfeld (1910) nearly always found the non-motile *Coccolithus pelagicus* phase of *Crystallolithus* associated with the *Pontosphaera borealis*. In fact Ostenfeld (1910) states he found both *Coccolithus pelagicus* and *Pontosphaera borealis* in the outer part of the pack ice and outside it, the *Coccolithus pelagicus* was dead (contents having been released—authors), but the *Pontosphaera* was most probably living when caught. Smayda (1958) supports this finding of the two phases occurring together by means of his records from around Jan Mayen Island where he reports the presence of *Crystallolithus hyalinus* and *Coccolithus pelagicus* 'at similar temperatures in the same habitat coupled with an identical habitus' to that in which Ostenfeld found the *Pontosphaera borealis*. It now appears certain that *Crystallolithus hyalinus* is synonymous with *Pontosphaera borealis* Ostenfeld.

The occurrence of a haptonema in a coccolithophorid was recorded by von Stosch (1955) for a form closely resembling, but not identical with, *Hymenomonas carterae* (Braarud & Fagerl.) Braarud. We have at the present time in culture in the Plymouth Collection three coccolithophorids, in addition to the *Coccolithus pelagicus*, which possess haptonemata. Two we have not yet related to any described species and the third is *Pleurochrysis scherffelii* Pringsheim (1955). In *P. scherffelii* the short haptonema is visible on the motile phase for only a very short period after release from the non-motile phase, since the coccoliths, which are produced gradually on the body surface, eventually mask it from view. This may also be the case for many other coccolithophorids and therefore many described forms may possess haptonemata which have not so far been detected, or alternatively, they have have been seen but not recognized in preserved material. For example, Prof. Chadefaud brought to our notice a paper by Schlauder (1945) in which she records three flagella in *Pontosphaera triangularis*, saying that the third flagellum appeared to be more rigid; it may therefore be a haptonema.

The secretion of coccoliths inside the cells of coccolithophorids has been recorded by a number of workers (see also p. 267), but the process by which they are produced inside the cell is still unknown. Prof. Manton's findings (Manton & Parke, 1960, p. 282 of this number) from the examination under the electron microscope of sections of a small green flagellate, which possesses surface body scales, may be the answer also to the internal production of coccoliths; she found inside the body of *Micromonas squamata* Manton & Parke evidence of the production of complete scales within more or less deep-seated vesicles. The large vesicles which appeared inside the *Coccolithus pelagicus* mother-cells prior to placolith deposition on the body surface suggest that coccoliths may originate in vesicles in a manner similar to scales.

There is little detailed and precise information available in the literature on the stages in the life history of coccolithophorids with the exception of the studies by Bernard (1948, 1949) on the life history of *C. fragilis* Lohm. Spore formation has been reported for some species and spores, morphologically different and more simple than the parent cell, have been recorded by Bernard (1938) for *Rhabdosphaera subopaca* Bern. and *Scyphosphaera elegans* (Ost.) Defl., suggesting that these two species may have a type of life history similar to the one we have recorded for *Coccolithus pelagicus*.

The few studies already published on the life history of coccolithophorids in culture—Braarud & Fagerland (1946), Pringsheim (1955), von Stosch (1955, 1958), and the present work—as well as our unpublished records from the ten species we have in culture, show undoubtedly that a great deal of valuable knowledge concerning the behaviour of these organisms (e.g. the demonstration of phagotrophy) and the stages in their life history can be obtained from the study of cultures.

Kamptner (1958), in his recent classification of the Coccolithineae, places the motile Crystallolithus phase of *C. pelagicus* in the tribe Syracosphaereae and the non-motile phase in the tribe Coccolitheae, both tribes being placed in the family Coccolithaceae. If this organism is classified on the micro-structure of its coccoliths, however, according to the units proposed tentatively by Braarud *et al.* (1955) and Halldal & Markali (1955), the motile Crystallolithus phase would be placed in the section with holococcoliths and the non-motile phase in the section with heterococcoliths. It appears, therefore, that a coccolithophorid, which produces two morphological types of coccolith, cannot be placed satisfactorily in the present systems adopted for the classification of the Coccolithophoridae, and so these systems need revision.

SUMMARY

The study of *Crystallolithus hyalinus* Gaarder & Markali in culture has shown it to be the motile phase in the life history of the non-motile *Coccolithus pelagicus* (Wallich) Schiller; two distinct morphological types of coccolith can therefore be produced by different phases of the one species.

Additional information from living material is given to supplement the original description of the Crystallolithus phase; sculptured scales are recorded under the crystalloliths in the hyaline outer layer of the body. This phase possesses a haptonema as well as two acronematic flagella; it exhibits phagotrophy and shows an unusual procedure for the discarding of waste material; its swimming and reproductive behaviour are recorded. The stages in the development of the *Coccolithus pelagicus* phase from the Crystallolithus phase are described. The occurrence of the two phases in the sea off Plymouth is recorded for the years 1957–59.

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EXPLANATION OF PLATES I–IV

Coccolithus pelagicus (Wallich) Schiller

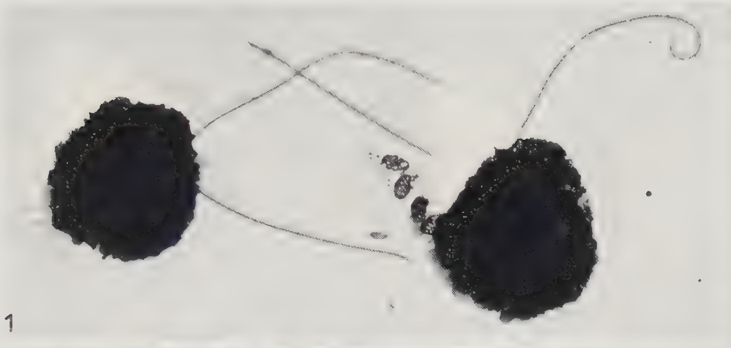
I

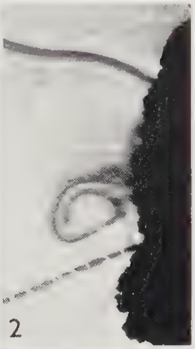
Electron micrographs of shadow-cast whole mounts taken with a Philips microscope carrying a 25 A pole-piece with astigmator, used at 60 kV.

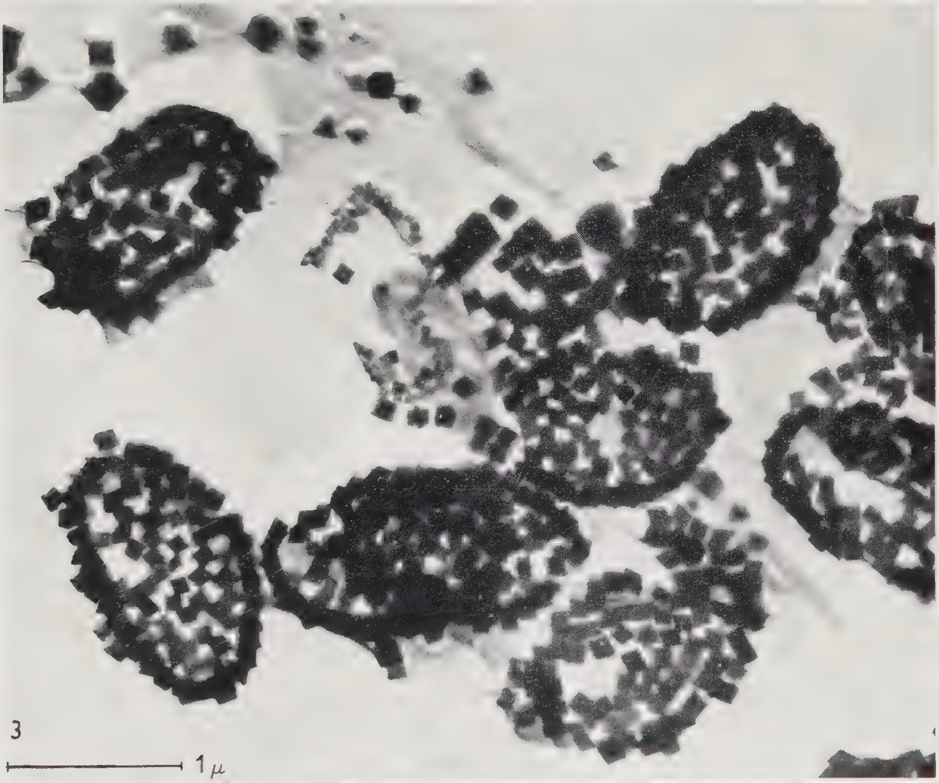
Fig. 1. Two Crystallolithus cells with bodies completely covered by crystalloliths. Exposure M 577.14, magnification × 1400.

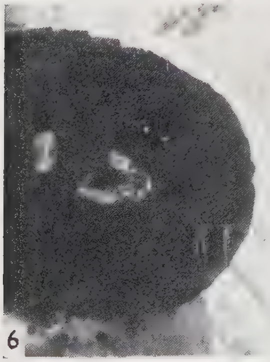
Fig. 2. Part of a Crystallolithus cell showing a coiled haptonema between the two flagella. Exposure M 577.17, magnification × *c.* 8000.

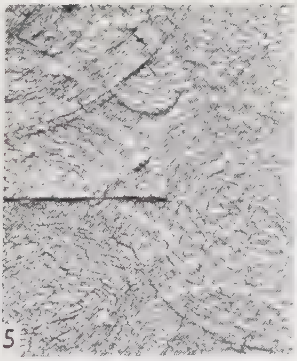
Fig. 3. Crystalloliths and translucent plate-scales from the motile Crystallolithus phase, direct print. Exposure M 577.6, magnification × 23,000.

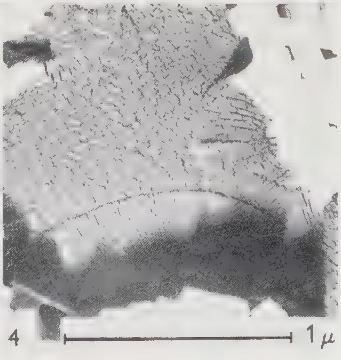












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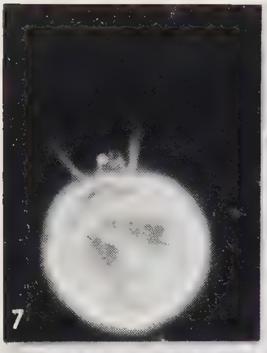
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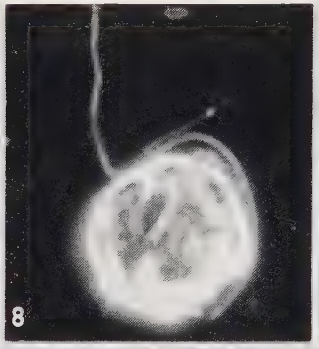
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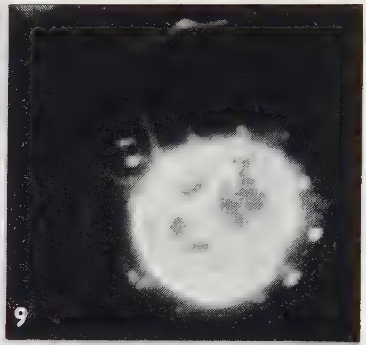
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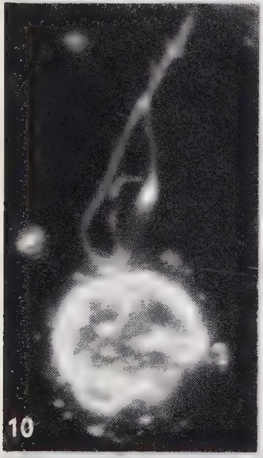
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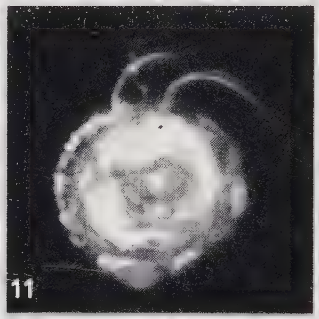
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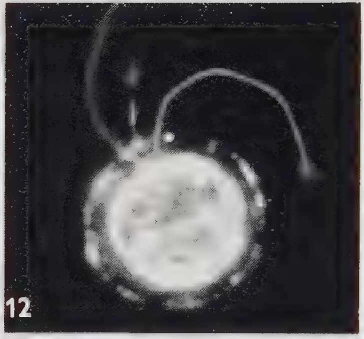
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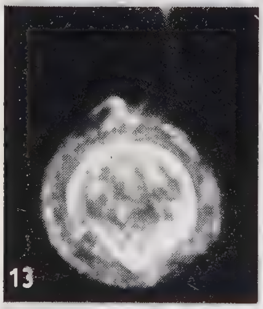
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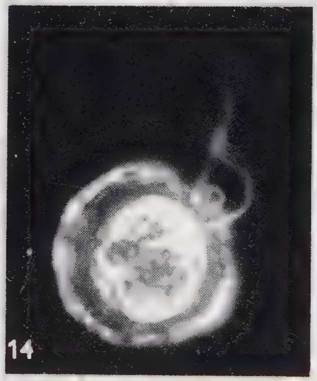
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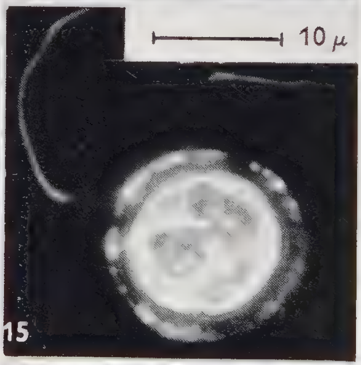
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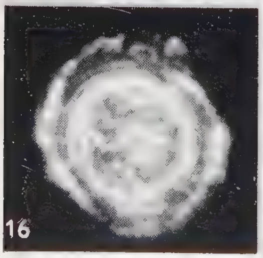
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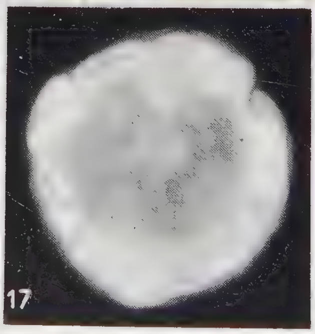
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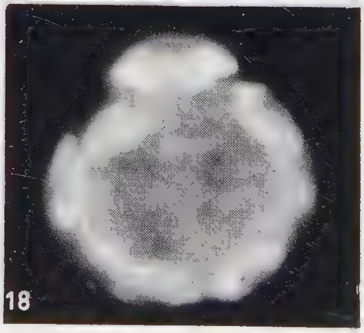
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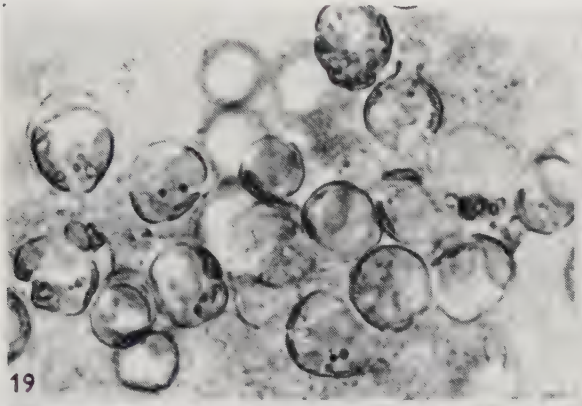
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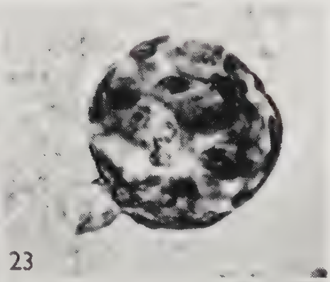
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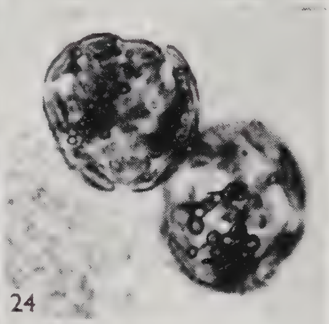
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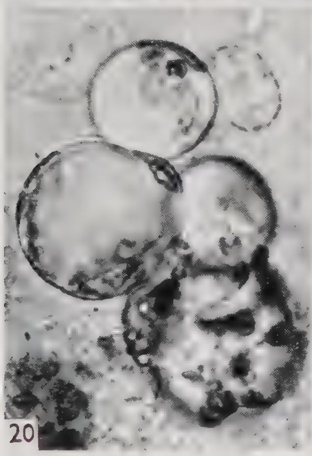
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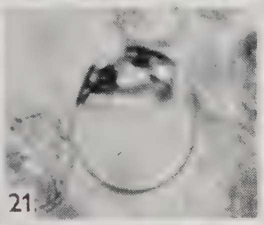
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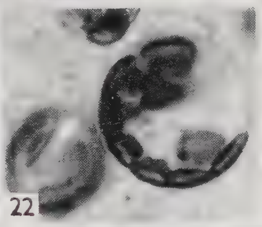
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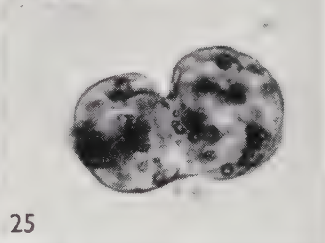
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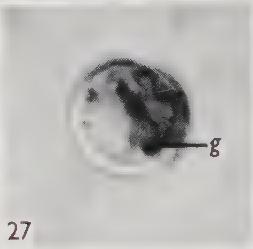
Figs. 19–25 20 μ

Figs. 26–30 20 μ



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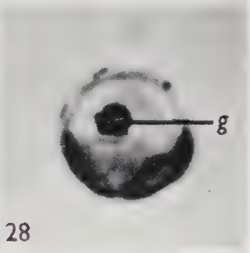

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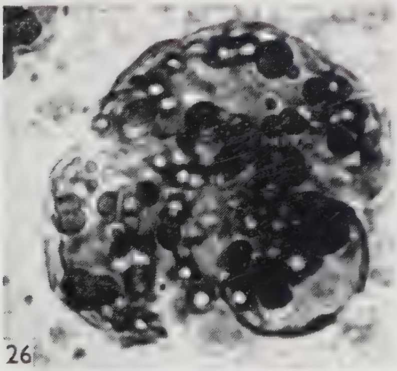
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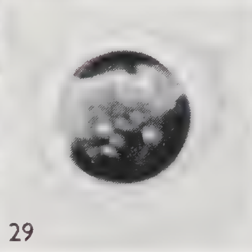
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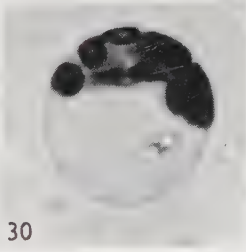
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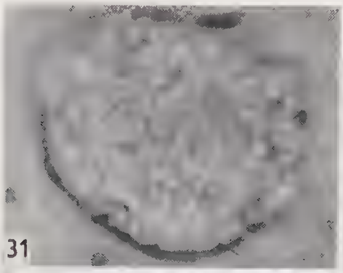
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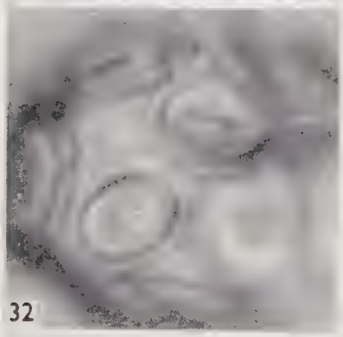
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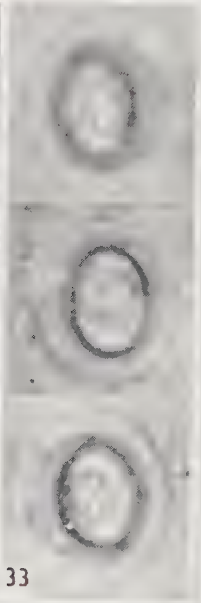
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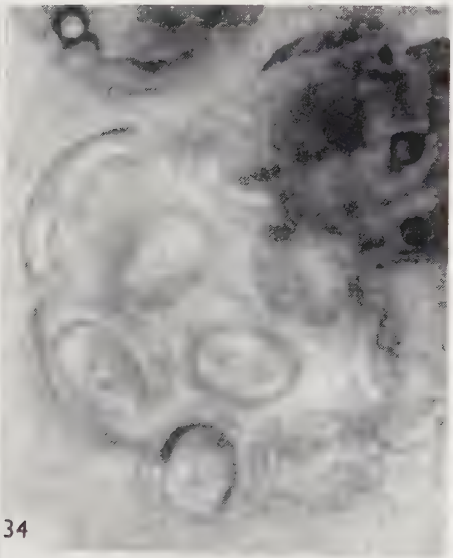
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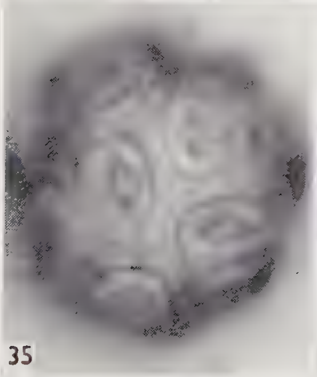
Figs. 31–37 10 μ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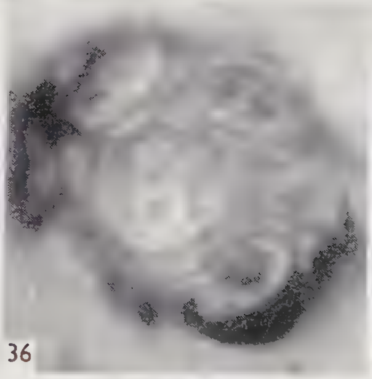
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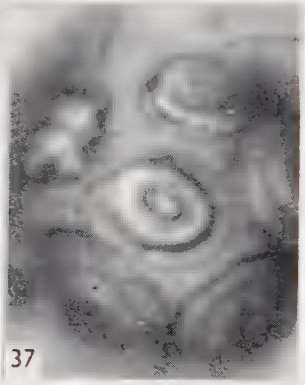
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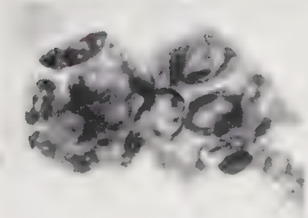
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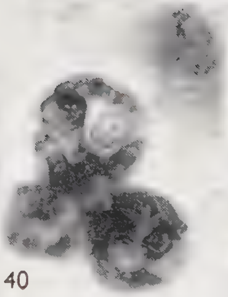
Figs. 38–42 20 μ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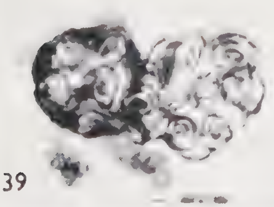
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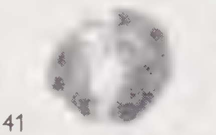
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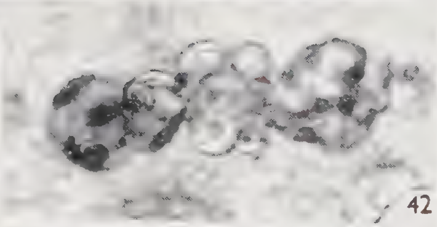
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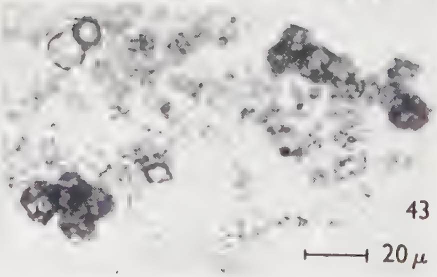
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20 μ

Fig. 4. Part of the field of fig. 3, reversed print, to show details of the markings on one side of the scales on which the crystalloliths are deposited. Exposure M 577.6, magnification × 30,000.
Fig. 5. Another field as fig. 4 but showing the markings on the other side of the scales. Exposure M 577.8, magnification × 30,000.
Fig. 6. Part of a placolith from the non-motile *Coccolithus pelagicus* phase. Exposure S. 686.7, magnification × *c*. 6000.

II

(Figs. 7–16, × 1650, Crystallolithus phase; Figs. 17, 18, × 1650, *Coccolithus pelagicus* phase.)

Fig. 7. Cell lacking visible hyaline layer round body; no crystalloliths formed.
Fig. 8. Cell with fully extended haptonema visible between the two flagella; very few crystalloliths present in outer thin hyaline layer of body.
Fig. 9. Cell with haptonema coiled and thin hyaline layer, few crystalloliths.
Fig. 10. Cell with two flagella, unequal in length, and haptonema fully extended; hyaline layer round body thicker than in fig. 9.
Figs. 11–14. Series of cells to show increase in thickness of hyaline layer round body and also the increase in the number of crystalloliths on the scales in this layer.
Fig. 15. Early fission stage.
Fig. 16. Non-motile Crystallolithus cell from bottom of a flask.
Fig. 17. Daughter-cell of *Coccolithus pelagicus* phase immediately after formation showing very thin hyaline layer covering the placoliths round the body.
Fig. 18. Same cell as fig. 17 after slight squashing to burst outer layer.

III

(Figs. 19–25, × 750; figs. 26–30, × 1250. Figs. 19–26, 29–30: stages in the development of the non-motile *Coccolithus pelagicus* mother-cell.)

Fig. 19. A group of non-motile Crystallolithus cells from a sample of the skin taken from the bottom of a flask.
Fig. 20. Four cells at different stages in development.
Fig. 21. Early stage with two chromatophores and very large leucosin vesicle.
Fig. 22. Later stage than fig. 21 with eight chromatophores and large leucosin vesicle.
Fig. 23. Mother-cell with lobed chromatophores at later stage than figs. 20–22, showing increase in size and disappearance of large leucosin vesicle.
Fig. 24. Two mother-cells with numerous small vesicles inside; cells fixed with osmium tetroxide.
Fig. 25. A mother-cell starting to divide before the placoliths are deposited on the body surface.
Fig. 26. A mother-cell dividing to produce four daughter-cells before the placoliths are deposited on the outside; many vesicles, darkened by osmium tetroxide, clearly visible inside the body; thin hyaline outer layer showing round part of the cell.
Fig. 27. A Crystallolithus cell showing a small pellet of ingested graphite (*g*).
Fig. 28. Another Crystallolithus cell showing a larger pellet of ingested graphite (*g*).
Fig. 29. A non-motile Crystallolithus cell showing a thick striated hyaline layer round the body.
Fig. 30. Slightly later stage (at higher magnification) than Fig. 21 with four dividing chromatophores and a large leucosin vesicle.

IV

(Figs. 31–37, × 2335; figs. 38–42, × 750; fig. 43, × 375.)

Fig. 31. Crystallolithus phase—empty hyaline casing containing the crystalloliths from which the daughter-cells emerged after fission of the parent-cell.
Fig. 32. Part of a *C. pelagicus* mother-cell, ovoid in shape, showing the overlapping of the placoliths on the body surface.
Fig. 33. Three placoliths from the *C. pelagicus* stage in surface view.

Fig. 34. A *C. pelagicus* daughter-cell squashed to liberate the cell inside the placoliths; liberated cell lying beside placoliths.
Fig. 35. A *C. pelagicus* daughter-cell, spheroidal in shape.
Fig. 36. A small *C. pelagicus* mother-cell, ovoid in shape.
Fig. 37. A *C. pelagicus* daughter-cell showing placoliths of normal and abnormal shape.
Figs. 38–39. First fission of *C. pelagicus* mother-cell.
Fig. 40. Second fission of mother-cell to produce four *C. pelagicus* daughter-cells.
Fig. 41. *C. pelagicus* daughter-cell from which contents have been liberated.
Fig. 42. Four *C. pelagicus* daughter-cells united together in a linear series, as described for a coccolithophorid by Wallich (1861, 1877).
Fig. 43. Low power photograph of groups of four *C. pelagicus* daughter-cells from sample of the skin taken from the bottom of a flask.

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FURTHER OBSERVATIONS ON SMALL GREEN FLAGELLATES WITH SPECIAL REFERENCE TO POSSIBLE RELATIVES OF *CHROMULINA PUSILLA* BUTCHER

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and M. Parke
The Plymouth Laboratory

(With total of 59 Figures on Plates I–IX and in text)

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INTRODUCTION

The observations to be recorded here have been carried out primarily for the purpose of clarifying the taxonomic position and naming of the small organism previously known as *Chromulina pusilla* Butcher. This had been shown (Manton, 1959*a*) to possess the pigments and fine structure appropriate to a position in or near the Chlorophyceae but quite inappropriate to a position within the Chrysophyceae to which the genus *Chromulina* properly belongs. Before selecting a new generic name, it was highly desirable to make some comparative electron microscopical observations on authentically named material of appropriate kinds since the fallibility of the light microscope for study of organisms of this order of size (1–3 μ) had been all too clearly exposed. A search was therefore made for a representative or representatives of the only genus of green flagellates known to us from the literature to possess a single posteriorly directed flagellum, namely *Pedinomonas*.

No species of *Pedinomonas* has so far been encountered among flagellates isolated from the sea at Plymouth, and most of those described in the literature have been from fresh water. The Culture Collection at Cambridge, however, contains two species referred to this genus, one a recent isolation from brackish water made by E. A. George who had provisionally identified it as *Pedinomonas minor* Korsch., and the other a freshwater species, *P. tuberculata* (Vischer) Gams.

When these two species were investigated electron microscopically it at once became apparent that they were so unlike each other that they could not possibly be regarded as representatives of one genus. This rather disconcerting discovery necessitated close attention to the taxonomic credentials of the two cultures since one showed many more points of resemblance to *Chromulina pusilla* Butcher than the other and therefore the correct allocation of the name *Pedinomonas* was a matter of critical importance.

There proved to be a substantial difference between the two cultures in the authenticity of the specific names attributed to them. The original culture of *P. tuberculata* had been presented to the Cambridge collection by the describer of the species and it still agrees with the published description (Vischer, 1945, 1949) in all details ascertainable with the light microscope; its specific identity cannot therefore be called in question. The other culture was, however, a recent isolate from British estuarine waters which had been named provisionally from the literature. Close comparison with Korschikov's original description (1923) of *Pedinomonas minor* (a freshwater species from Poland) soon convinced us that though superficially similar our material could not be this species. Moreover, the differences detectable with the light microscope, notably those concerned with the character of the starchy food store, were also differences from the situation found in the culture of *P. tuberculata*. Since *P. minor* Korschikov itself is generally assumed to be the type species of *Pedinomonas* we are forced to conclude that the material supplied to us under this provisional name is not only not this species but is a new and undescribed species of an, at present, untypified genus.

The fine structure of our new species is, however, similar in many respects to that of *Chromulina pusilla* Butcher, allowance being made for a difference in cell size. There are also substantial morphological differences, notably in the long hair point terminating the flagellum in the latter and the very unusual covering of scales on the flagellar surface in the former; but as long as we have, as at present, only one species of each type on record, and since some of the characters in which the two species differ most from each other are completely invisible with the light microscope, it seems not unreasonable in the present state of knowledge to regard these differences as specific and not as generic criteria. It is then possible to construct a new generic diagnosis which will separate both these species from *Pedinomonas minor* on light microscope characters and from *P. tuberculata* on light microscope and electron microscopical characters.

We therefore propose to describe our new species as *Micromonas squamata* sp.nov., referring it to *Micromonas* gen.nov. of which *M. pusilla* (Butcher) comb.nov. will be the type. In designating *M. pusilla* and not *M. squamata* as the type species of *Micromonas* we are hoping to safeguard *M. pusilla* from further name changes should it become necessary in the future to subdivide this genus.

Our observations contribute only indirectly to an understanding of *Pedinomonas* itself since we still lack electron microscopical information about the type species. We therefore propose to limit the account of *P. tuberculata* to the minimum necessary to substantiate our view that generic separation from *Micromonas* is essential. It will be possible to deal briefly with *M. pusilla* since all the electron microscopical facts have already been placed on record in Manton (1959*a*). Our new species, *M. squamata*, will however be described as fully as is normally necessary in dealing with a new species, and since the fine structure has in this case been of critical importance in indicating the probable affinities we propose, in the account which follows, to present the electron microscopical evidence first. To meet the needs of the light microscopists, however, and to facilitate cross-reference we have supplied a table (p. 292) listing all the more important specific characters of all three species and have assembled together (Pl. IX and p. 291) all the photographs and drawings made with the light microscope instead of following our usual practice of grouping these beside the electron micrographs of the species to which they refer.

We are able to dispense with a special section on material and methods since the methods used are exactly the same as in our previous studies on marine flagellates (Parke, Manton & Clarke, 1955, 1956, 1958, 1959; Manton, 1959*a*) and the few additional details about our sources of material will be inserted with the specific descriptions.

OBSERVATIONS WITH THE ELECTRON MICROSCOPE ON *MICROMONAS SQUAMATA* SP.NOV.

External morphology

Low-power views of intact cells are uninformative except as evidence of size (Fig. 1). The single posteriorly directed flagellum is about 12 μ long and though it is sometimes accompanied by a second, or even a third (Fig. 2) or fourth flagellum, such supernumeraries being of any length from very short to equal, there is no doubt that these all relate to growth stages of cells in division or to giant cells representing double-divisions. In normal undivided cells, which make up the majority in any culture, only one flagellum is present.

At higher magnifications (Figs. 3–6, 7–8) the scales and other surface appendages become visible. Almost always the arrangement of scales is disturbed by the act of drying the preparation though they commonly remain in close proximity to the surface from which they have fallen. These surfaces include not only the body of the cell but the entire length of all flagella from their base to extreme tip as may be seen in the various specimens included in Figs. 3–6. Only one of the five individual flagella depicted, namely that of Fig. 5, shows the scaly covering intact. In this particular specimen the flagellar axis has shrunk in drying and has therefore drawn away from the tubular sheath of scales which covers it. The scales themselves in this sheath are, however, still in their original positions and the regular imbrication over the entire surface is a striking feature; the few loose scales present in the field near this flagellum come almost certainly from the body of the same cell.

The fine structure of the scales is best shown in Figs. 7 and 8. There is a considerable range of sizes on any one cell, but all show a highly characteristic spider's-web pattern which we have not previously encountered on the other organisms described by us.

In addition to scales, many flagella also show hairs of an unusual kind. They are sometimes present in abundance on both sides of the flagellum and others emerge from the tip as in Fig. 4. The lateral hairs seem to fall off very

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Explanation of Plates I–VI

Micromonas squamata sp.nov.

I

Fig. 1. A dried cell photographed with the light microscope. × 1000.

Fig. 2. A double-division cell with three flagella photographed with the light microscope. × 1000.

Fig. 3. Tips of two of the flagella of fig. 2, the apex of the right flagellum damaged, that of the left flagellum intact, both showing a layer of detached scales throughout their length. Electron micrograph S 702.15, × 15,000.

Fig. 4. Tip of another flagellum to show presence of hairs as well as scales. Electron micrograph S 668.37, × 20,000.

Fig. 5. Tip of an unusually well preserved flagellum with the scaly covering intact and showing their regularly imbricated arrangement. Electron micrograph M 586.4, × *c.* 30,000.

Fig. 6. A flagellar tip showing detached hairs and scales and three long terminal hairs replacing the attenuated apex of the left-hand specimen in fig. 3. Electron micrograph H 4867, × 30,000, reversed print.

II

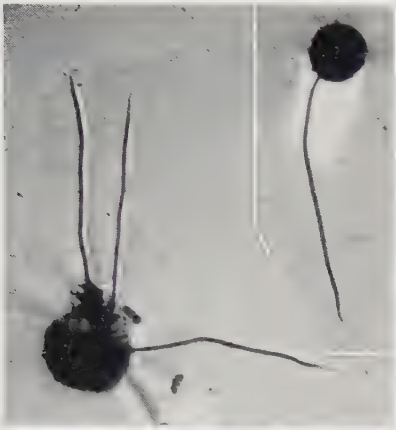
Fig. 7. Detached hairs and scales. Electron micrograph S 680.18, × 50,000, reversed print.

Fig. 8. Detached scales. Micrograph H 5760, × 70,000, reversed print.

Fig. 9. Part of a TS of a cell with two flagella transected near it; covering of imbricated scales visible on both. Micrograph H 246, × 30,000.

Fig. 10. LS of a flagellum attached to the body and showing imbricated scales in position over it. Micrograph H 2833, × 30,000.

Figs. 11, 12. Thick sections of two cells transecting the chloroplast in directions approximately at right angles; the translucent area around the core of the pyrenoid visible in both; the nucleus present only in fig. 11. Micrographs S 690.24 and 20, × 12,000.



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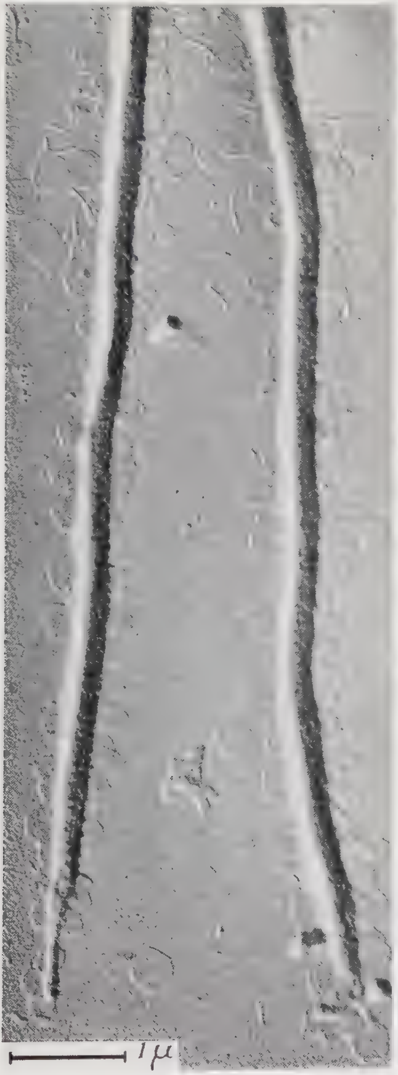

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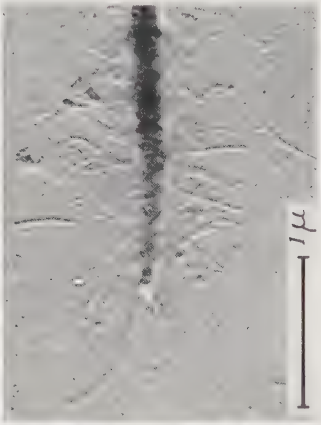

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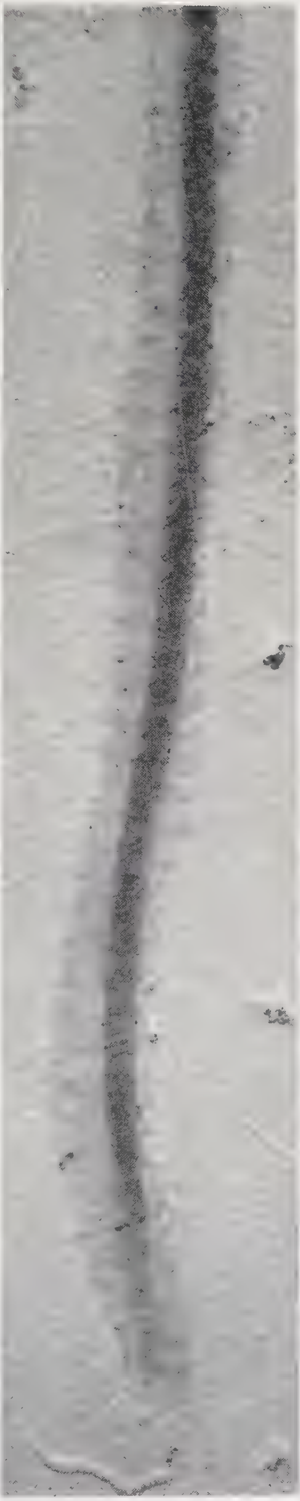

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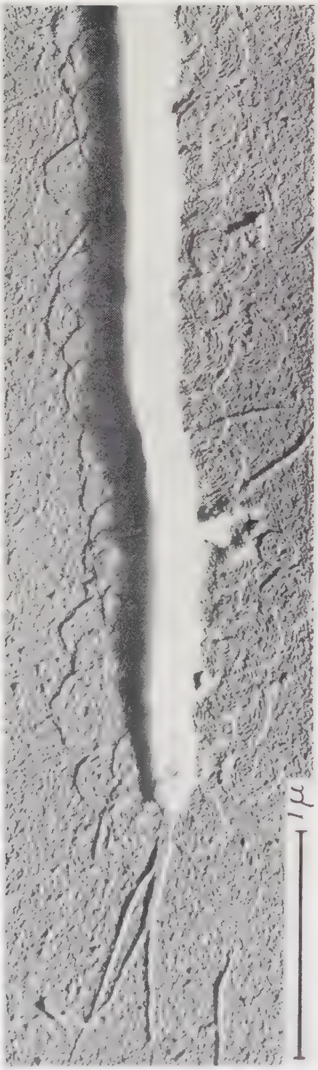

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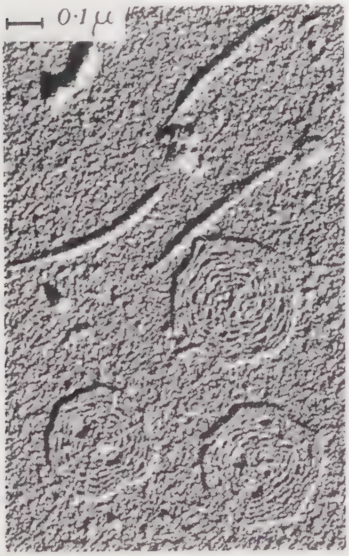

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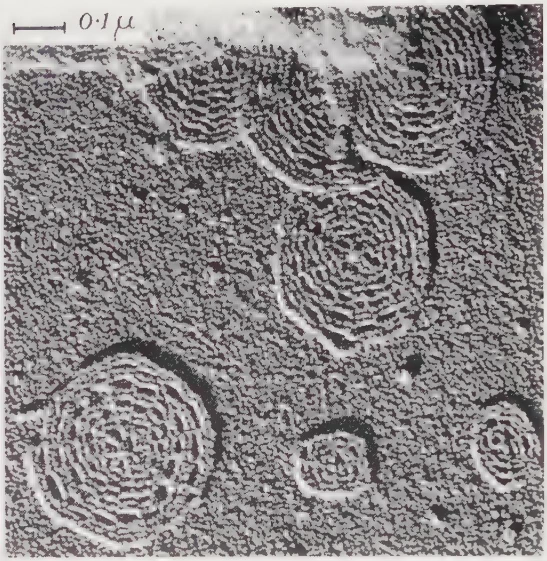

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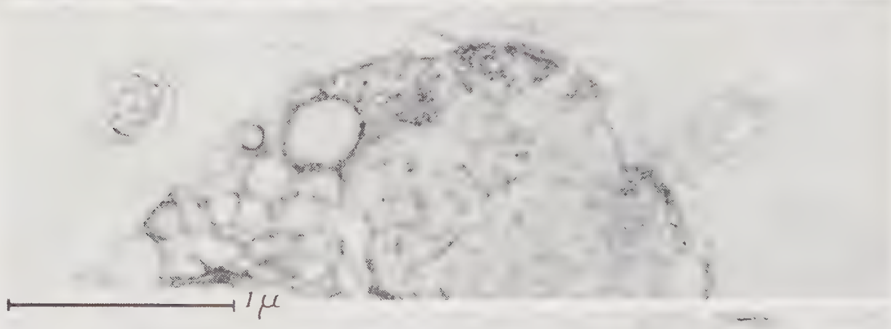

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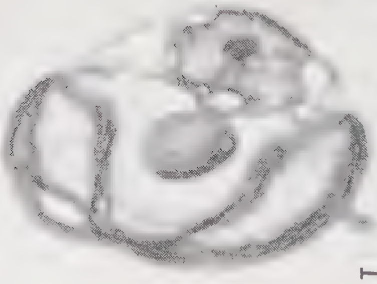

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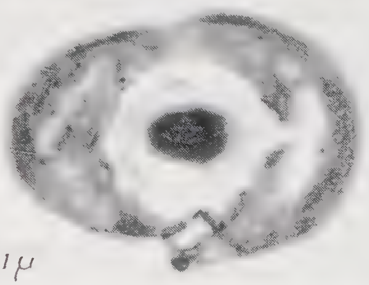

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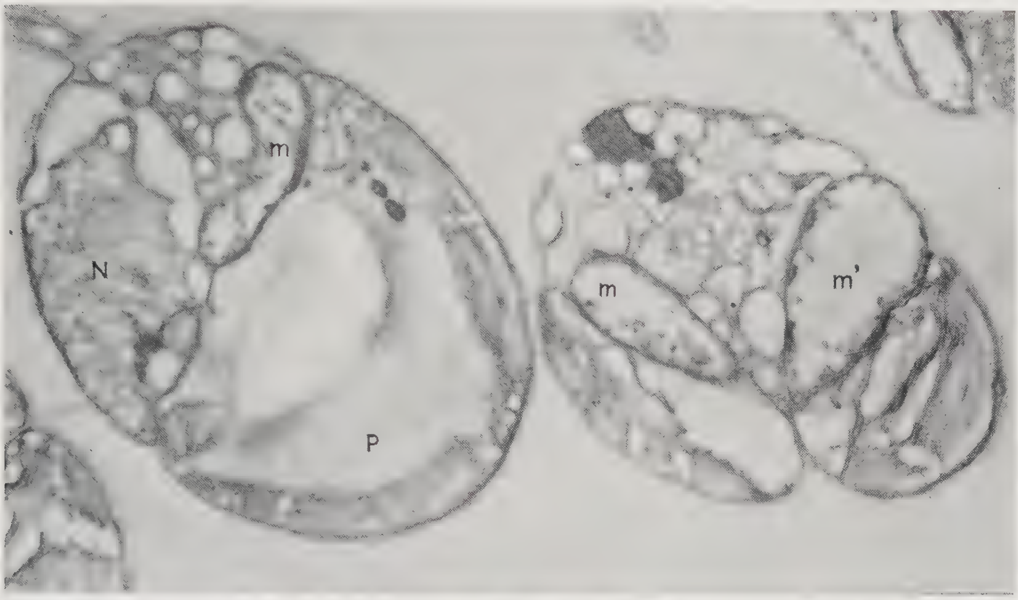

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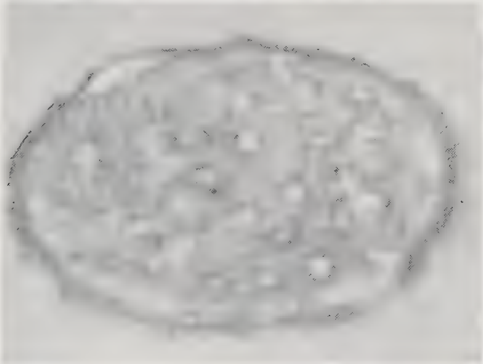

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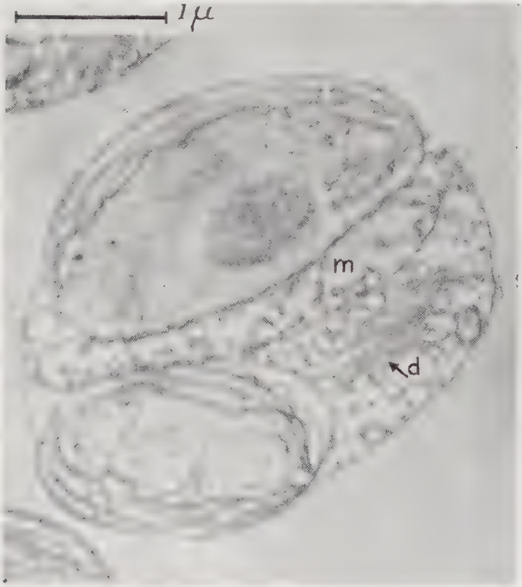

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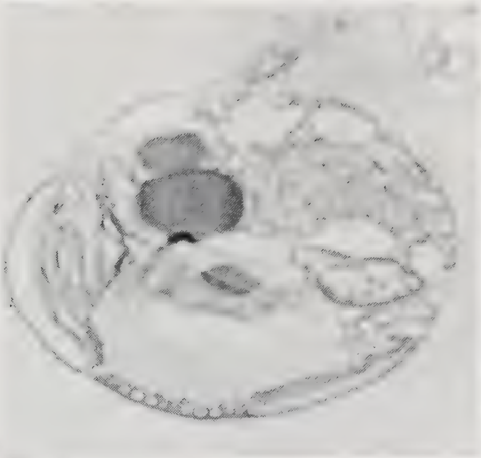

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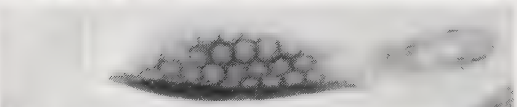

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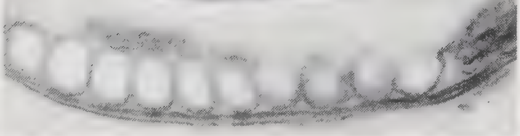

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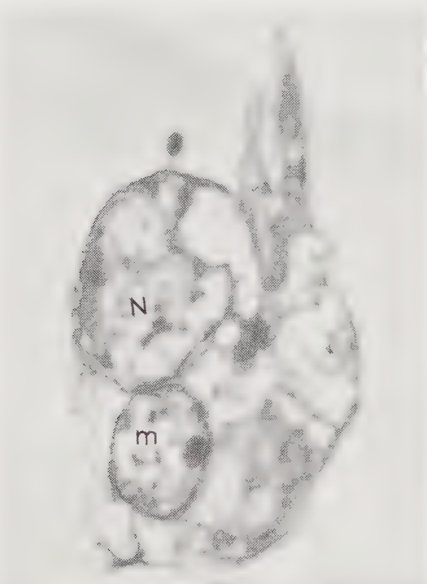

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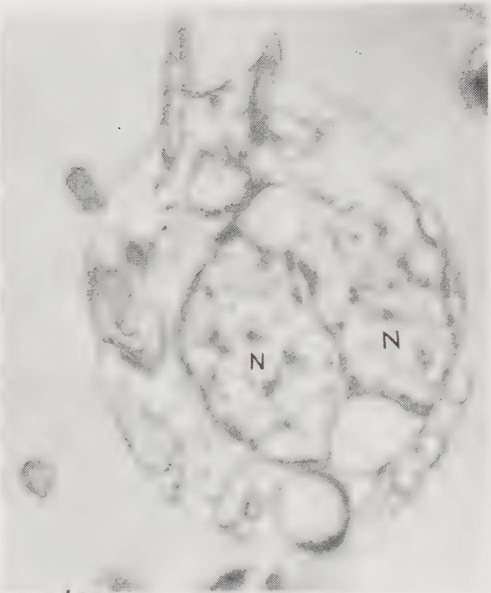

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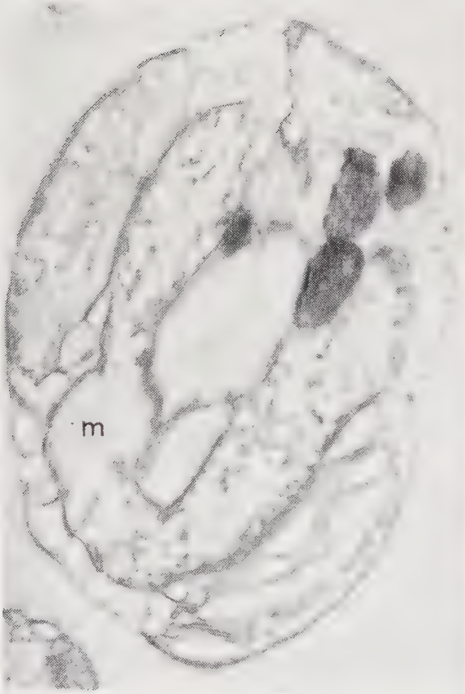

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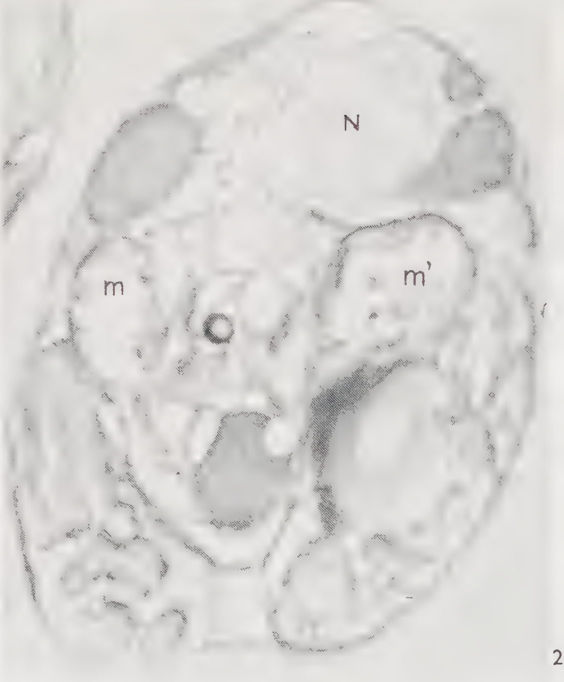

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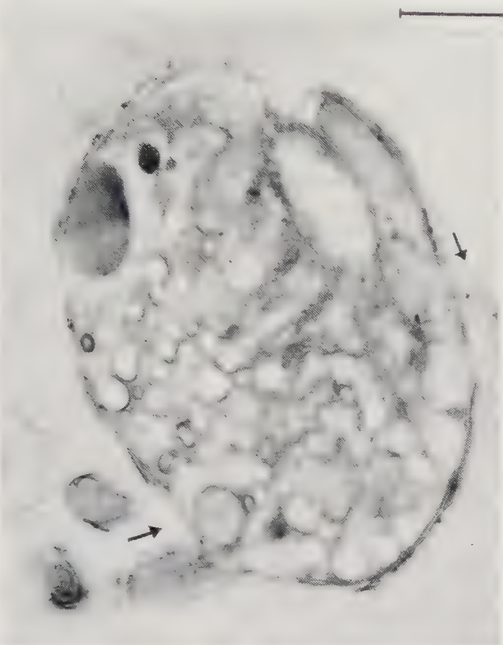

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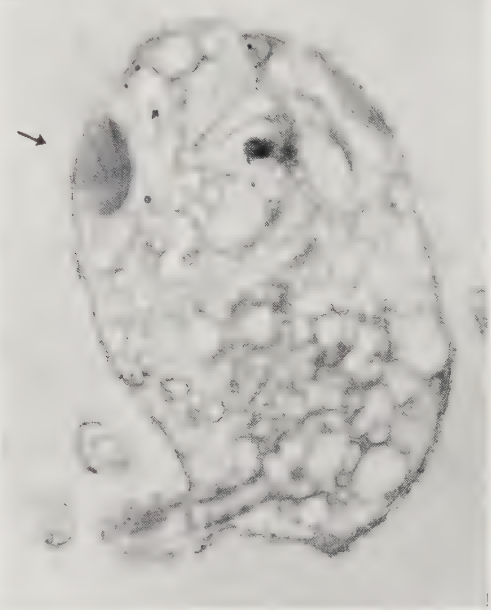
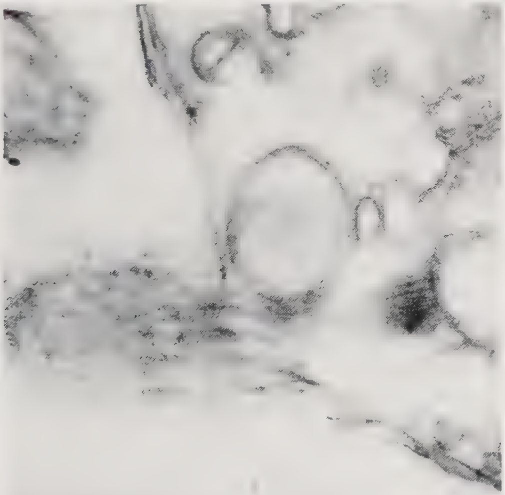


23b



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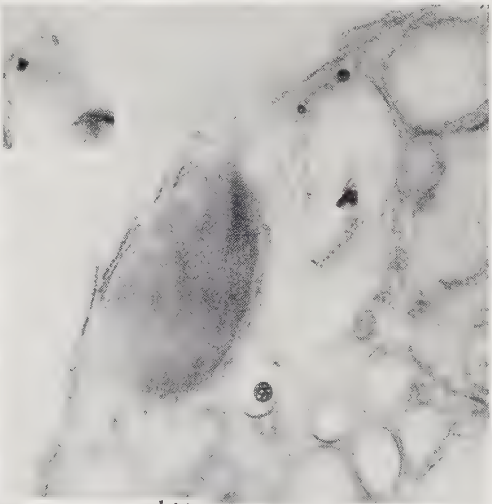

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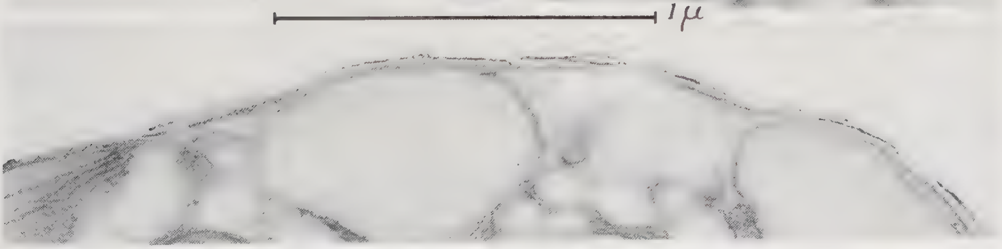

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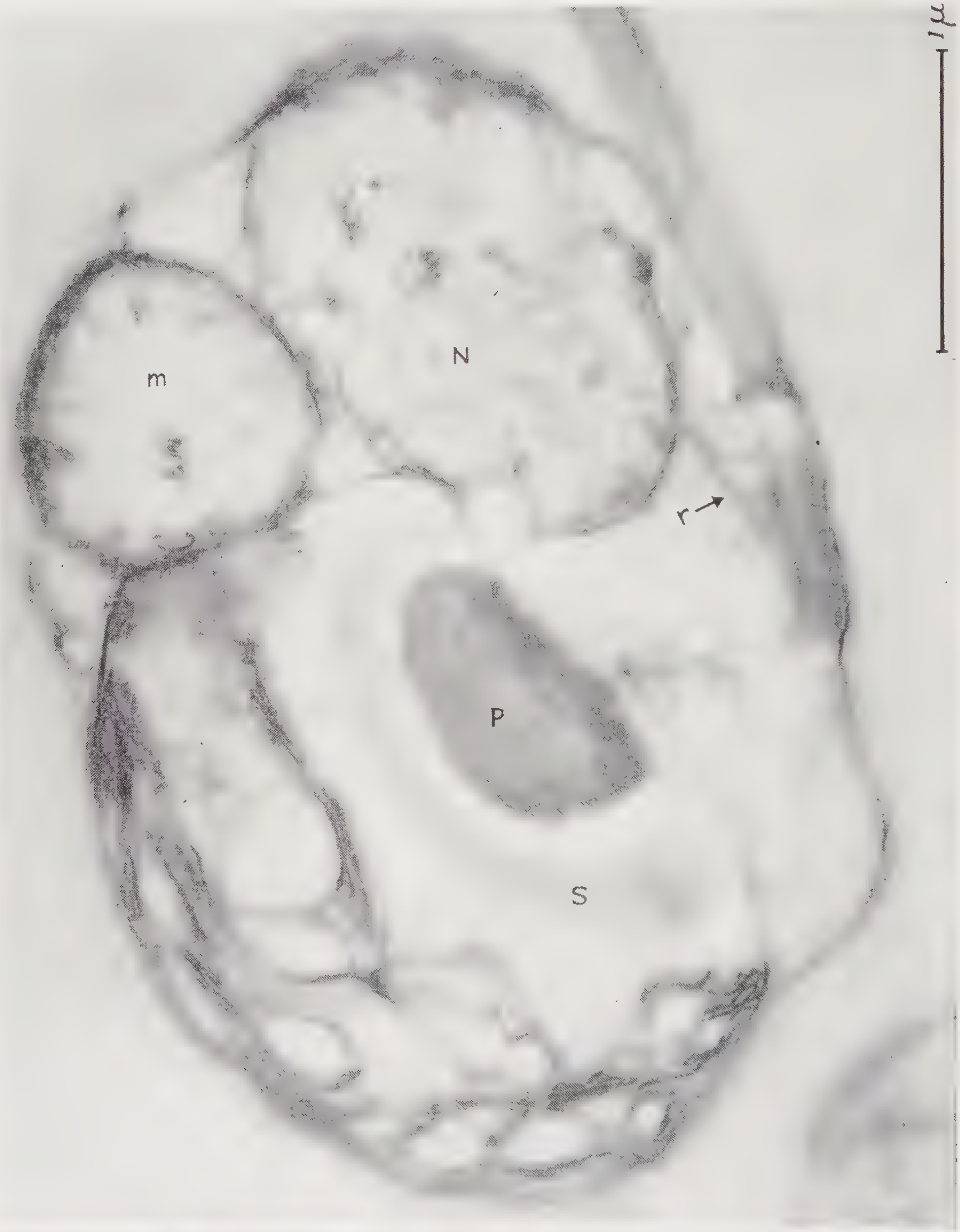

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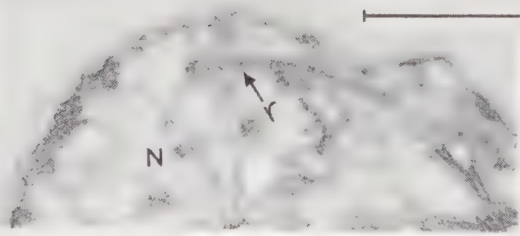

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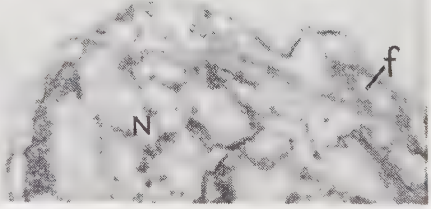


29b

Explanation of Plates I–VI continued

Micromonas squamata sp.nov.

III

Fig. 13. Two cells, the left-most passing through the nucleus (*N*), the mitochondrion (*m*), the plastid (*P*) cut near but not through the pyrenoid and showing the stacks of paired plastid lamellae near the surface with fenestrations at intervals; the right-hand cell a division stage with two lobes of a bent U-shaped mitochondrion (*m* and *m'*) associated with the two halves of the plastid (another section of this cell, not reproduced, showed the centre part of the mitochondrion connecting the two lobes). Micrograph H 247, × 20,000.

Fig. 14. Tangential section near the surface of a plastid showing the fenestrations in face view. Micrograph H 5777, × 20,000.

Fig. 15. Part of a dividing cell showing golgi (*d*) and a long arm of a mitochondrion (*m*) between two plastids. Micrograph H 5467, × 20,000.

Fig. 16. A section passing through the plastid to show a structure resembling an eyespot (bottom centre) but without sign of pigment. Micrograph H 2728, × 15,000. For further details of eyespot region see figs. 17 and 18.

Fig. 17. Tangential section near the surface of a plastid in the region of the putative eyespot showing the close-packing of objects resembling pigment chambers, an obliquely cut flagellum near. Micrograph H 5777, × 20,000.

Fig. 18. More highly magnified view of plastid surface with putative pigment chambers covered by plastid double-membrane and cell body membrane. Micrograph H 2635, × 50,000.

IV

Figs. 19, 20. Two successive stages of a division showing different degrees of separation of the two flagella for the daughter-cells; two nuclei side by side visible in fig. 20. Micrographs H 2995 and H 3010, × 20,000.

Fig. 21. Stage in a cell-division showing a very long U-shaped mitochondrion (*m*) between two plastids or plastid lobes. Micrograph H 242, × 20,000.

Fig. 22. Another specimen at a stage similar to that of fig. 21 but cut in a slightly different plane and showing two plastids (or plastid lobes), a nucleus (*N*), a U-shaped mitochondrion (*m*, *m'*) with the arms in contact with the two plastids, some fat bodies and vesicles with other contents in the trough of the U. Micrograph H 698, × 20,000.

V

Fig. 23*a*, *b*. Two successive sections through a flagellar insertion cut near the surface of a cell and showing disposition of vesicles and other details represented more highly magnified in figs. 24–26. Micrographs H 2647 and H 2639, × 20,000.

Fig. 24. Part of the section of fig. 23*a* near the flagellar base showing a vesicle containing a scale in full face view immediately above the flagellar insertion. Micrograph H 2647, × 50,000.

Fig. 25. A scale in face view outside the body for comparison with that of fig. 24, from the region of the arrow on the right of fig. 23*a*. Micrograph H 2647, × 50,000.

Fig. 26. Part of the cell surface showing imbrication of body scales, from the field near the arrow in fig. 23*b*. Micrograph H 2639, × 50,000.

Fig. 27. Imbricated scales on the surface of part of another cell. Micrograph H 2639, × 50,000.

VI

Fig. 28. LS of a cell passing through the pyrenoid *P*, the starch shell *S*, the nucleus *N*, the mitochondrion *m* and showing the fibrous connection (*r*) between the base of the flagellum and the nuclear surface. Micrograph H 2986, × 40,000.

Fig. 29*a*, *b*. Two adjacent sections through another specimen showing the fibrous connection (*r*) from the flagellar base (*f*) ending on the nuclear surface (*N*). Micrographs H 5459 and H 5461, × 30,000.

easily, but even when none are retained on the flagellum itself they are always to be found scattered on the field in the neighbourhood, e.g. Fig. 3, top centre. It seems necessary to believe therefore that they are normal structural features and not fixation artifacts.

The average length of the lateral hairs is of the order of half a micron and their width approximately 200Å; they are therefore relatively coarse, considerably more so than bacterial flagella. They are usually slightly curved with one end attenuated; this end appears to be that by which the hair is attached to the flagellum. These features are well seen on some of the detached hairs included in the field of Fig. 7.

The tuft of hairs at the tip of the flagellum is perhaps of a different nature. The tips of flagella in general are known to be specially sensitive to post-mortem changes and it is not always self evident which condition of several which may occur is the least altered. In the present material it seems likely that the apex of the left-hand flagellum of Fig. 3 is in fact in the most undamaged state since it corresponds in general shape to the normal condition in many other organisms. On the right-hand flagellum of Fig. 3 the tip is partly broken away, while the abrupt termination of the flagellar column immediately below the terminal tuft of three hairs in Fig. 6 suggests that these particular hairs may perhaps be part of the distal extremity of the flagellar axis from which the outer skin has been removed leaving three of the longest component fibrils within it exposed. If this interpretation is correct the terminal hairs would here correspond to the internal parts of the attenuated distal apex of the left-hand flagellum of Fig. 3; if incorrect it would be necessary to assume that a terminal garniture of three hairs has in fact been present on the tips of all these flagella but in the case of those in Fig. 3 has fallen off. The first alternative is the more probable.

Internal structure

A preliminary view of most of the essential body organs can perhaps best be obtained from the most highly magnified section, reproduced in Fig. 28. This is comparable in attitude and plane of cutting with Fig. 11 of Manton (1959*a*) and the strong resemblance to the arrangement and structure of the cell of *Chromulina pusilla* Butcher will at once be apparent if the two are examined together. There is the same large plastid with superficial lamellations and conspicuous eccentric pyrenoid with dark central contents surrounded by shells of lighter material. There is the same single mitochondrion, and the positions relative to the flagellum of both these organs and of the nucleus are also comparable. The cells of our present species are, however, considerably larger (3–6·5 μ instead of 1–3 μ) and therefore certain features, notably the fibrous root connecting the base of the flagellum with the surface of the nucleus, can be demonstrated here relatively easily though looked for in vain in the smaller organism. This root is visible in Fig. 28, and two adjacent sections of another specimen are reproduced in Figs. 29*a* and *b*. The root undoubtedly terminates on the nuclear surface without either passing beyond or penetrating it. The distal tip is perhaps covered by a spirally wound sheath since diagonal lines sloping in opposite planes are detectable in the two sections (Figs. 29*a*, *b*).

The only other constant organs not included in Fig. 28 are fat bodies, seen incidentally in several other sections, notably Figs. 13, 16, 21 and 22, and golgi areas (dictyosomes), one of which is indicated in Fig. 15. A single dictyosome is always present near the flagellar base, as in the previous species.

Within these various organelles certain additional structural details deserve attention. The structural arrangement within the plastid is perhaps more clearly revealed by the two thick sections cut in planes approximately at right angles to each other included in Figs. 11 and 12 which amplify previous information on the general shape and distribution of storage and pigment materials. The thinner sections of Figs. 13 and 14 add further details of the pigmented layers. Thus in Fig. 13 (left) the section misses the pyrenoid but passes perpendicularly through the pigmented layers showing them to be stacks of paired lamellae interrupted at intervals by spaces which in surface view (Fig. 14) appear as roughly isodiametric holes scattered in a fairly uniform distribution over the surface.

Figs. 16–18 show some of the details associated with the region resembling an eyespot in the middle of the outer surface of the plastid. Here the ordinary lamellae are replaced by a layer of close-packed cylindrical chambers with well marked walls resembling those encountered in eyespots of other organisms, e.g. *Fucus* (Manton & Clarke, 1956), though here with translucent contents suggesting that special pigmentation was either absent at the time of fixation or has dissolved out.

The region of the putative eyespot is very suitable for demonstrating the compound nature of the plastid membrane (Fig. 18). Its over-all thickness is somewhat greater than that of the cell-body membrane overlying it which is also compound (better seen underlying the scales in Fig. 27).

The single mitochondrion, which is in itself one of the more striking features by which this species resembles *Chromulina pusilla* Butcher, is very strikingly shown in the early division stages during which the mitochondrion may become very long and bent into a U or V shape before dividing. Different manifestations of this are included in Figs. 13, 21 and 22, but it should be noted that if the plane of section does not coincide with the plane of elongation of the mitochondrion the two ends may be found so far apart (e.g. Fig. 13) that at first they might be mistaken for two separate organelles. That this is not so is clearly indicated by the constant position of the component parts lying in what is effectually a groove between the plastid rim and the centre bulge caused by the pyrenoid and marking the eventual place of cleavage. The number of cristae, i.e. internal projections within the mitochondrion, is far larger than in *C. pusilla*; they appear to be somewhat flattened tubes, rather short and not displaying the peculiar curved paths characteristic of the other species (Manton, 1959*a*).

The most important new facts from the point of view of a general understanding of algae are those associated with the origin of the scales. It is probable that the scales are slightly mineralized since, though no thicker than the scales of the species of *Chrysochromulina* described by us, they are slightly more opaque than these when seen in section (e.g. Fig. 27), appearing distinctly denser than the cell membrane over which they lie. This circumstance makes them slightly more conspicuous in various planes of section than the unmineralized scales more familar to us and it is probably for this reason that the following observations as to their mode of formation have been obtainable. It had previously been thought probable that scales of any kind when encountered on the surface of a 'naked' cell would have been produced in one way or another from the surface membrane underlying them. That this is not so here is however proved by finding completed scales inside the cell as in Fig. 24 where a perfect spider's-web scale is encountered in face view in the centre of a large vesicle below the cell surface near the insertion of the flagellum. Figs. 23*a* and *b* are introduced to show the exact position on the specimen from which this detail was taken and other scales outside the body or in position on it are illustrated in Figs. 24–26. Since all attempts to demonstrate phagotrophic feeding by this species have proved vain it is necessary to conclude that internal scales are part of a developmental process and have not been swallowed from outside.

It has not been possible to follow all the developmental details, since scales can scarcely be recognized as such in a very incomplete condition. The probable site of synthesis is, however, in the group of vesicles with contents which commonly occupies the space between the arms of a V-shaped mitochondrion in a dividing cell (Fig. 22). These vesicles contain contents of various kinds including, usually, some densely opaque material and also objects possessing a type of refringence reminiscent of that of the scales. If this is a true identification these vesicles are too large and too full of contents to be engaged in production of single scales. It therefore seems probable that the early stages are passed through in groups within these large, relatively central, vesicles, and that the transferrence of single scales into separate vesicles near the cell surface is part of the final act of deposition. If this is so the very regular imbrication of the scales covering the flagellum, already seen in Fig. 5 and detectable both in LS and TS in Figs. 9 and 10, is readily understandable as the expression of the successive opening on to the surface of a cluster of vesicles each containing one scale and arranged round the base of a growing flagellum. The great difficulty of imagining any mechanism by which scales could be produced from the apparently normal flagellar surface itself is thereby eliminated.

OBSERVATIONS WITH THE LIGHT MICROSCOPE ON *MICROMONAS SQUAMATA* SP.NOV.

Examples of cells photographed with the light microscope, using dark-ground illumination, will be found grouped under one number as Fig. 40, Pl. IX (facing p. 288); some are in the uniflagellate condition and the remainder are division stages with two or four flagella, unequal to equal in length. Fig. 39, Pl. IX, illustrates two cells of *Chromulina pusilla* Butcher at the same magnification for comparison; their much smaller size has made it impossible to obtain effective photographs of the flagella by this method.

Cells of the organism that we propose to name *Micromonas squamata* sp.nov. can swim fairly quickly, rotating rapidly with only slight gyration and moving in straight lines for short distances, but more usually they move fairly slowly with slow rotation of the body and more pronounced gyration. They can also glide along for short distances without rotation, or they can show periods of jerking about very actively by the lashing of the flagellum. During movement, the region of the body at which the flagellum arises is always foremost. The proximal 1–2 μ of the flagellum becomes pulled out into what appears, when the cell is moving, to be a short stiff spine-like organ which lies in *front* of the body (Figs. 44–45); the remainder of the flagellum is curved sharply backwards down the side of the body to lie behind the cell. When cells are moving rapidly the flagellum appears to vibrate but when moving more slowly definite undulations can be observed; the undulations are usually small but can on occasion be large. A cell stops swimming suddenly by bringing the flagellum up with a sharp jerk of the body into a curved position round and under the body (Fig. 42), sometimes coiled twice round the body (Fig. 43), after which the cell will commonly move off in a different direction. In fission stages when a second flagellum has developed, the two behave homodynamically, both twisting round the body simultaneously when a cell stops swimming to change direction.

The region of the body close to the point of origin of the flagellum can show considerable metaboly and, in addition, fine pseudopodium-like filaments have several times been seen produced; they appear to attach to the surface of the slide but so far only cells in the incipient fission stage have been seen producing these filaments (Fig. 46).

In an actively growing culture 15% of the cells are 3 μ in size, 20% 3·5 μ, 40% 4·0 μ, 13% 4·5 μ, while the remaining 12% are incipient fission stages ranging from 5 to 6·5 μ in size. The smallest cells (newly divided daughter-cells) may show some slight flattening of the body but the larger cells and the fission stages are more globose. The flagellum length in relation to the body size can vary from $2\frac{1}{2}$ to 4 times the length of the body but 80% of the cells have a flagellum $3–3\frac{1}{2}$ times the length of the body.

This organism shows a distinct phototactic reaction but there is no evidence of phagotrophy. In culture it is yellow-green, i.e. is similar in colour to *Chromulina pusilla* Butcher, and it contains, as does the latter, chlorophyll *a*, chlorophyll *b*, β-carotene and α-xanthophyll (Dr G. Y. Kennedy, personal communication).

In the living cell the most obvious of the cell contents are the chloroplast with its embedded pyrenoid and, when present, the refractive lipid body or bodies. The chloroplast is situated on the side of the body opposite to that from which the flagellum arises; under the high power it appears striated with the pigmented outer region crescentic in optical section. The pyrenoid, immersed in the inner side of the chloroplast, is surrounded by a starch shell staining violet with iodine. The starch shell shows considerable variation in shape and size in different cells and it may be studied either in intact stained cells or loose among the debris taken from broken cells at the bottom of the flask. Examples of such isolated but intact starch shells are drawn in Fig. 47. When least developed the starch shell is a hollow sphere a little over 1 μ in diameter surrounding the pyrenoid on all sides except that nearest to the unpigmented face; an isolated starch shell is therefore a hollow sphere with a hole at one pole. As the shell thickens its outline becomes more ovoid and irregular, the starch appearing to be laid down unevenly, more being deposited on the sides than in the centre but the hole on the inner plastid face never becoming covered. The largest starch shells are about 3 μ in diameter.

There is usually one lipid body, about 0·5 μ in diameter, situated in the cell on the side opposite to the chloroplast, but occasionally none are present. After a culture has been grown in strong light for some time additional lipid globules can be seen in the cells; there may be from 1 to 4 and they lie against the inner face of the chloroplast. The stigma, orange-red, and oval to oblong in the surface view, measuring up to 1 × 0·5 μ, lies centrally in the outer face of the chloroplast and is not always readily detected. A single elongated mitochondrion, 1 × 0·75 μ in size when stained with Janus Green, lies on the inner face of the chloroplast while the ovoid nucleus, 1·5 × 1 μ in size, lies outside it towards the side of the cell from which the flagellum arises. The golgi area, situated close to the nucleus, stains with Janus Green to give a bluer colour than the mitochondrion. Neither the body scales nor the flagellar scales stain with cresyl blue, but the flagellar basal body can be detected after fixation with osmium tetroxide.

Asexual reproduction can occur in either the motile or non-motile phase. In the motile phase fission is usually into two daughter-cells but it is not uncommon for double-fission to occur producing three or four daughter-cells at the same time from the parent cell (Figs. 40, 48, 49). The first indications of fission are the simultaneous elongation of the stigma and pyrenoid accompanying the first appearance of the second flagellum; occasionally the stigma divides and the daughter-flagellum appears before the elongation of the pyrenoid. By the time the daughter-flagellum has nearly reached its full length the nucleus, mitochondrion, golgi, chloroplast, pyrenoid and stigma have divided. The daughter-flagellum is fully developed and the chloroplasts have separated before actual fission of the body commences at the flagellar pole. In the non-motile (palmelloid) phase, the cells become surrounded by what appears to be a very thin membrane lying close to the body; such cells divide into four or occasionally eight daughter-cells (Figs. 50, 51). The apparent membrane shows up a little more clearly after treatment with Schultz's solution but its precise nature is uncertain.

If this description is compared with that of Korschikov (1923) for *Pedinomonas minor* the following differences from *P. squamata* should be noted: habitat in standing fresh water of inland areas in Poland and west Russia (more recently reported from similar habitats from Hungary by Fott & Ettl (1959)), in contrast to the brackish habitat of *M. squamata*; presence of a contractile vacuole reported in *P. minor*, not detectable in *M. squamata*; the flagellum in *P. minor* considerably shorter (only $1\frac{1}{2}$ times body length) than in *M. squamata* (where it is $2\frac{1}{2}$–4 times body length); starch grains present round the pyrenoid as opposed to the continuous starch shell of *M. squamata*.

OBSERVATIONS WITH THE ELECTRON MICROSCOPE ON *PEDINOMONAS TUBERCULATA* (VISCHER) GAMS

External morphology

The cells of this species make very elegant preparations when dried down and they also possess an unusual capacity for informative dismemberment. One intact cell is illustrated in Fig. 30 with the tip of its plume-like flagellum shown more highly magnified in Fig. 33. The profuse garniture of very delicate hairs spread on the field on both sides of the flagellar axis are highly characteristic. They are individually so slender, however, that the bacterial flagella lying loose in various parts of the field of Fig. 31 appear coarse in comparison.

Where cells have dismembered as in Figs. 31 and 32, four stout roots arranged in a cruciform manner are seen to be attached to the lower end of the flagellar base. These roots have a fibrous core and a membranous covering which in some if not all exhibit conspicuous diagonal striations as of a spiral winding of alternating bands of different electron opacity. This diagonal cross-banding is clearly visible in the lowermost root of Fig. 32.

Internal structure

One morphological detail, namely, the superficial tubercles from which this species gets its name, is better seen in sections than in our whole mounts. They occur as spine-like excrescences on various parts of the body as may be seen in Figs. 34–35. These tubercles are covered by the normal body membrane and they therefore represent local deposits of material beneath the membrane. This material is unidentifiable by the electron microscope alone but the presence of cellulose, calcite and quartz (SiO_2 in micro-crystalline form) has been indicated by X-ray analysis by Brandenburger & Frey-Wyssling (1947) and one or other of these components could be represented here. In addition, the surface membrane, which bears no resemblance in section to a normal cell wall, is covered by small spicules and traces of amorphous material among which fine particles of metallic osmium commonly become lodged as a fixation artifact. It therefore seems probable that though entirely devoid of either scales or a cell wall of algal type the membrane of this species is not completely naked on its outer side.

When viewed in section (Pl. VIII) the cells of *P. tuberculata* appear strongly flattened. Internally the cell is dominated by the large starch-filled chloroplast which is here curved (see especially Fig. 37), surrounding the other cytoplasmic organs which lie in the hollow. In a section cut in another direction (Fig. 36, approximately at right angles to Fig. 37) the nucleus is seen to be strongly flattened against the outer surface of the body on one side. There are several rather small mitochondria in the hollow of the curved plastid, one conspicuous golgi body (dictyosome) near the flagellar insertion and an array of small vesicles and granular cytoplasm. A few larger vesicles containing traces of opaque fat-like material are often conspicuous, though

Explanation of Plates VII and VIII

Pedinomonas tuberculata (Vischer) Gams

VII

Fig. 30. A dried cell. Micrograph S 672.26, × 3000.

Fig. 31. Field containing a dismembered cell represented by an intact flagellum with four roots arranged in a cruciform manner; bacterial cells and bacterial flagella loose upon the field and appearing relatively coarse in comparison with the very fine lateral hairs on the flagellum of *Pedinomonas*. Micrograph S 669.30, × 10,000.

Fig. 32. Base of the flagellum and roots from another specimen showing fibrous structure in the roots and traces of cross-banding probably carried by a covering membrane on the longest of the roots shown. Micrograph S 669.29, × 20,000.

Fig. 33. Tip of the flagellum of the cell of fig. 30 more highly magnified to show the details of the hairs. Micrograph S 672.28, × 20,000, reversed print.

Fig. 34. Section through a tubercle. Micrograph H 4957, × 30,000.

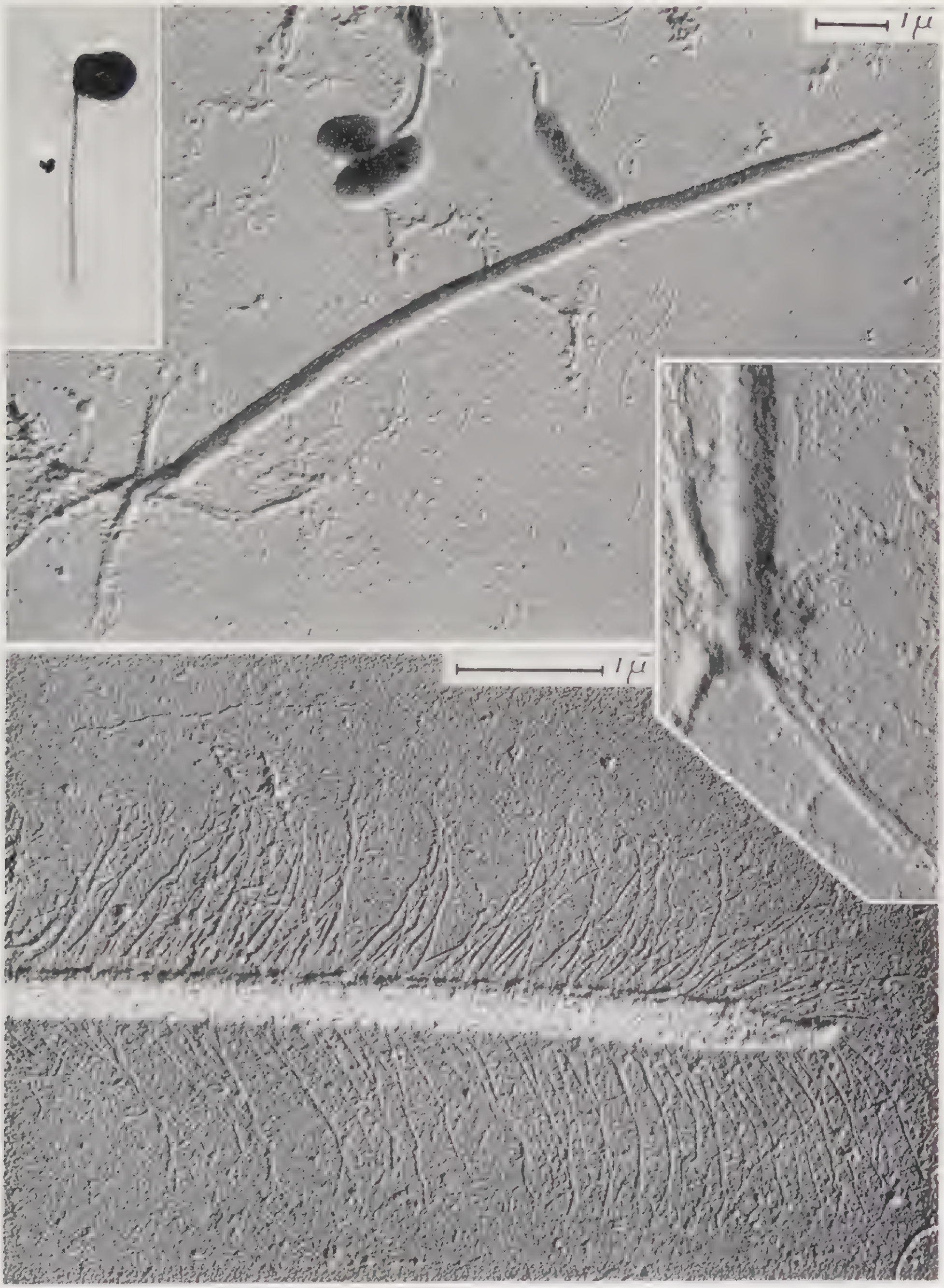
Fig. 35. Section through a tubercle, another specimen. Micrograph H 4985, × 40,000.

VIII

Fig. 36. Section of a cell showing parts of all the main organelles; nucleus (*N*), pyrenoid (*P*) starch grains (*S*), mitochondria (*m*), golgi (*d*). Micrograph H 4993, × 40,000.

Fig. 37. Section cut in another plane showing the curved plastid surrounding the other organelles in the hollow, the flagellar base cut transversely at the top of the section. Micrograph H 5047, × 30,000.

Fig. 38*a*, *b*. Two successive sections through a flagellar base (*f*) in the region of a root (*r*), to show its superficial position and close relation with the edge of the plastid; a golgi area (*d*) also included in Fig. 38*b*. Micrographs H 4981 and H 4978, × 50,000.



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31

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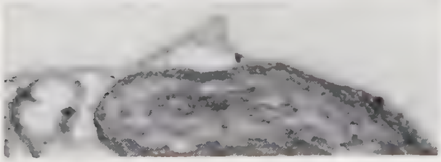

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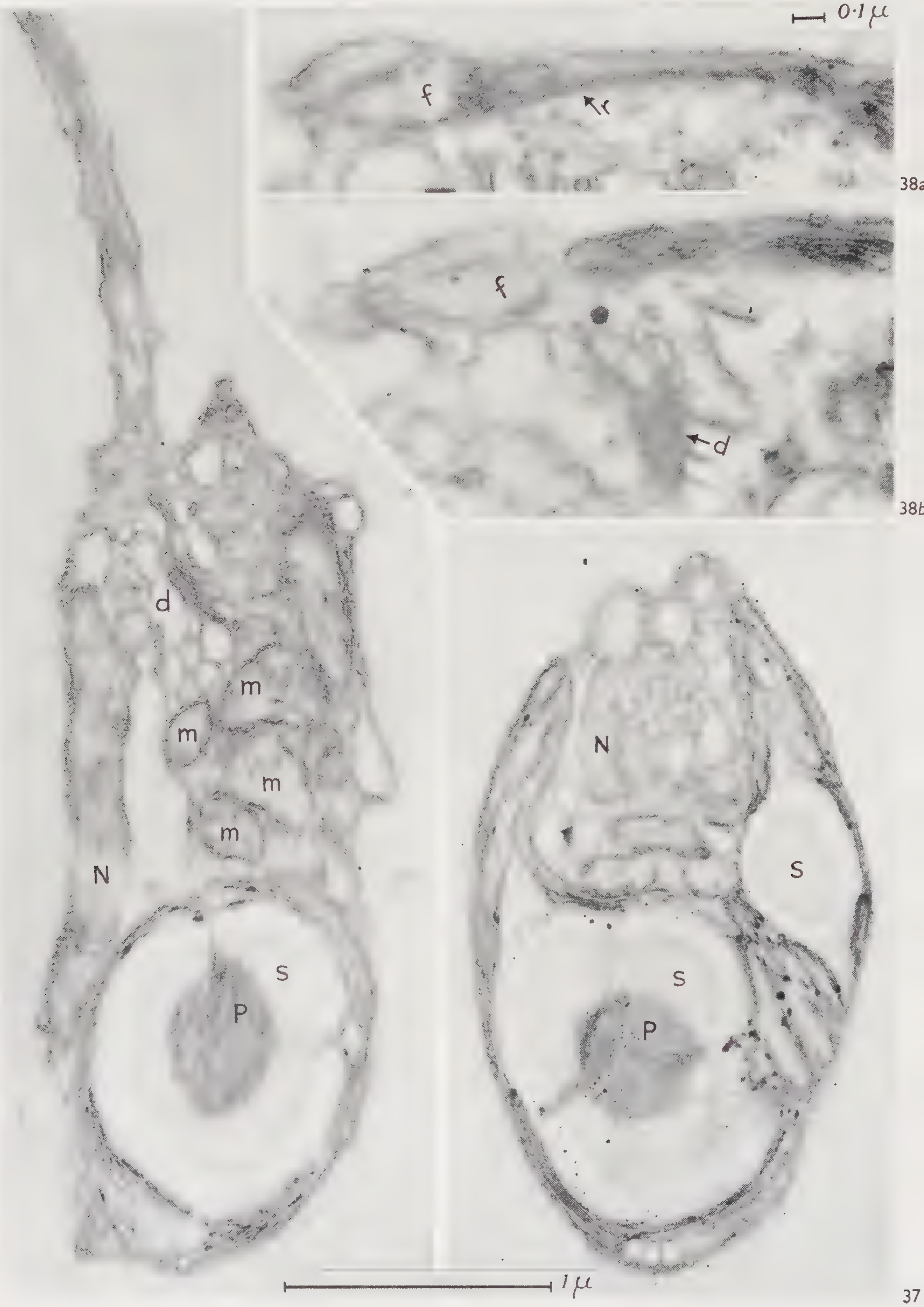
35


0·1 μ
f
r
38a
f
d
38b
d
m
m
m
m
N
S
P
N
S
S
P
36
1 μ
37

not included in the section reproduced. The cavity at first suggestive of a large vesicle on the right of the nucleus in Fig. 36 is a distortion of the perinuclear space.

Within the plastid the stacks of paired lamellae are conspicuous outside and between the starch accumulations; dark granules are conspicuous among them and there are traces of fenestrations comparable to those of *Micromonas squamata* here and there (Fig. 36). The pyrenoid itself has a dense core traversed by channels connected with the lamellated surface; large starch grains occupy the space between the lamellae and the core. Additional starch grains occur singly in other parts of the plastid (Fig. 37).

Some details concerning the attachment of the flagellum are illustrated in Fig. 38*a* and *b*. The flagellum itself is situated close to one edge of the plastid, as may clearly be seen in the specimen transected in Fig. 37. Fig. 38*a* shows the position of one of the cross-banded roots in relation to the subtending basal body (*f*). This root (*r*) remains close to the cell surface running along the plastid edge (cf. Fig. 38*b*) and apparently terminating on it (Fig. 38*a*). There is no sign of a direct attachment to the nucleus which in this particular specimen is situated in the direction of the bottom right-hand corner of Fig. 38*b*. The disposition of the other three roots is uncertain and it is possible that some may proceed in the direction of the nucleus, but it is probable that all are relatively superficial in position since this would adequately explain the ease with which they tear out of the cell when it dismembers.

This species thus differs from *M. squamata* in the shape of the plastid and structure of the pyrenoid, in the possession of conspicuous starch grains both in the pyrenoid and outside it, in the size, number and position of the mitochondria, in the position and shape of the nucleus, in the nature of the cell surface, and in the character and mode of attachment of the flagellum.

OBSERVATIONS WITH THE LIGHT MICROSCOPE ON *PEDINOMONAS TUBERCULATA* (VISCHER) GAMS

Vischer's descriptions (1945, 1949) are sufficiently accurate and detailed to make it unnecessary for us to quote many new observations on *P. tuberculata*. The presence of chlorophyll *a* and chlorophyll *b* has been demonstrated by Harder & Koch (1954), but even though both species of *Micromonas* also contain these pigments there is a readily perceptible difference of actual colour, *P. tuberculata* being a bright grass green both in the mass and in individual chloroplasts, whereas both species of *Micromonas* appear no more than yellowish green. The presence of starch in definite grains round the pyrenoid and elsewhere in the chloroplast is easily attested by staining with iodine.

A small eyespot as claimed by Vischer can sometimes be seen, ovoid in shape, 0·5–1·0 μ long and pale orange-red in colour, situated centrally on the surface of the plastid (Fig. 52). It is not, however, always detectable and the extreme insensitivity of the organism to the direction of incident light added to our inability to detect an eyespot structurally in the sections so far examined with the electron microscope suggests that perhaps the pigment spot observed may be of some other kind.

The organism swims fairly rapidly, travelling sometimes in straight lines for short distances or sometimes in circles; stops are frequent, the flagellum then curving towards the body (Fig. 54), after which the cell will move off in the same or another direction. During movement the body rotates and can show considerable gyration. The flagellar insertion is always directed backwards during swimming with the flagellum trailing (Figs. 41, 52, 53). The insertion itself is slightly off centre (Figs. 52–54).

FURTHER OBSERVATIONS WITH THE LIGHT MICROSCOPE ON *MICROMONAS (CHROMULINA) PUSILLA* (BUTCHER) COMB.NOV.

The following new observations on living cells may be quoted to supplement the account of the fine structure already published (Manton, 1959*a*). The cells can be very fast moving, with frequent changes of direction (relative speed in culture quoted by Knight-Jones & Walne (1951) as fifty times the body length per second). When a cell changes direction it frequently moves round in circles for a time before swimming off in a different direction. During rapid swimming the cell travels with the rounded end, containing the chloroplast, foremost and with the clear end curved towards the side from which the flagellum arises (Fig. 55). The flagellum proper is then at right angles to the body, arising from the concave surface and with its distal long hair-point curving outwards and backwards (Figs. 55, 56); the shape of the whole cell is then strongly reminiscent of a comma. It is probable that the body does rotate when the cell is swimming very rapidly, but rotation can be seen only when movement becomes slower since there seems to be no gyration. The cells can also swim for short periods with the flagellum directed forwards (Figs. 57, 58) but the speed is then slower. This species characteristically has considerable periods of remaining in one position attached to a surface by the clear end of the body which tends to show metaboly, the cell

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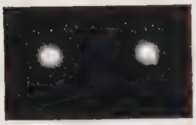
Explanation of Plate IX

Photographs of cells under oil immersion with the light microscope arranged for dark ground illumination, all magnified × 1000.

Fig. 39. Two cells of *Micromonas pusilla* (Butcher) comb.nov., the small tubercle on the right-hand cell is the flagellum, its hair-point not visible.

Fig. 40. *Micromonas squamata* sp.nov. A series of exposures to show the uniflagellate condition and various division stages.

Fig. 41. *Pedinomonas tuberculata* (Vischer) Gams. A series of exposures to show uniflagellate cells and division stages.



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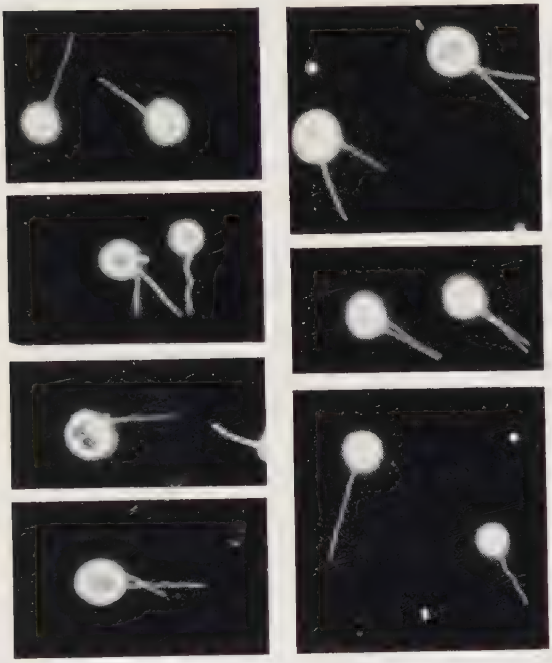

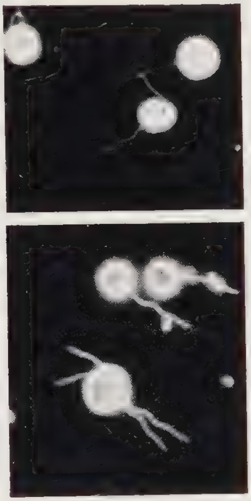

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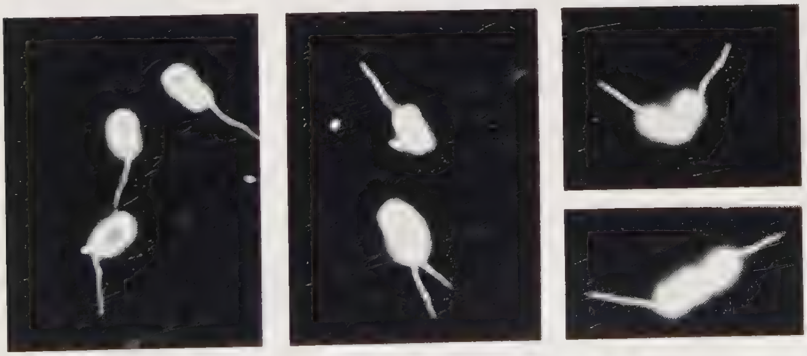

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(*Facing p.* 288)

meanwhile either swinging round in circles from the point of attachment (Fig. 59) or exhibiting a dithering movement which is very characteristic for this organism.

The species is strongly phototactic and is not toxic to fish (tested by Mrs B. Hepper). Motile cells in culture measure 1·0–3·0 μ long × 0·75–1 μ wide. Fission occurs in both motile and non-motile condition. A non-motile palmelloid phase with cells measuring 2·5–5 μ and showing a translucent area round each also occurs, the cells dividing into 2 or 4. No trace of cellulose is detectable in either motile or non-motile phases and no positive signs of starch when tested with iodine. Signs of a sexual process have been looked for by mixing five different strains, without success.

In occurrence this marine flagellate is very widespread; it has been recorded from surface samples taken from estuaries, creeks and the open sea around the British Isles (Knight-Jones, 1951, 1952; Knight-Jones & Walne, 1951). According to Knight-Jones it is the most generally abundant organism in British coastal waters and the North Sea, the greatest density he recorded for it being 3500 cells per ml in October 1946 from the Helford River, Cornwall.

Our records, covering a period of several years (Tables 1 & 2, Appendix) amplify those of Knight-Jones and Walne and show that this species occurs commonly in the English Channel throughout the year from the surface down to 70 m (Table 2). It occurs also in oceanic water and has been recorded from oceanic stations from the surface down to a depth of 500 m (Table 1). In Table 1 of the Appendix (p. 297) its occurrences are listed other than for International Station E1 and Plymouth Laboratory Stations L 2–6 from 17 September 1957 to 8 September 1959, the records for which are included in Table 2 (p. 297). This table includes densities at different depths sampled on one day at International Station E1.

SUMMARY OF TAXONOMIC CONCLUSIONS AND DIAGNOSES

We can now summarize in tabular form the more important facts ascertained or verified by us for the three organisms under discussion. From this table (p. 292) it will be seen that the organism formerly known as *Chromulina pusilla* Butcher agrees with *Micromonas squamata* in all salient features of internal organization, including plastid structure and form, the possession of one mitochondrion and in the position, relative to other cell organs, of the single flagellum. It differs in the absence of a scaly covering, in the absence of any trace of lateral hairs on the flagellum and in the very unusual relative proportions of the flagellum and its hair-point.

In contrast, *Pedinomonas tuberculata* differs from both the other species in the shape of nucleus and chloroplast, in the position and number of the mitochondria, in the presence of starch in definite grains, in the presence of canaliculi traversing the core of the pyrenoid, in the possession of tubercles beneath the surface membrane and of traces of calcite, quartz and cellulose indicated by X-rays in association with the body membrane, and perhaps most of all in the morphology and mode of attachment to and within the cell, of the flagellum with its four large roots attached apparently to the chloroplast rather than to the nucleus and its very profuse array of exceptionally delicate hairs down the two sides. The resemblance between *P. tuberculata* and either of the other species is limited to very general features such as the plastid pigments, which are similar in all three in spite of the apparent difference of colour when viewed under the microscope, and to the possession of a single chloroplast and a flagellum directed backwards in swimming though arriving at this position in a somewhat different way. This degree of resemblance is perhaps sufficient to permit the placing of *P. tuberculata* within the same family or class as the other two species though not in the same genus.

It is not necessary for us to discuss the genus *Pedinomonas* further here, except to point out the strong probability that all the characters enumerated above as differentiating *P. tuberculata* from our other two species may need to be added to the specific diagnosis of *P. tuberculata* if the time ever comes to characterize this genus more fully in terms of its proper type species. With regard to our new genus *Micromonas* we are in no doubt that this can be

Legends to Text-figs. 42–59, all × 5,000

Micromonas squamata sp.nov.

Fig. 42. Cell stationary with flagellum curved round under body in characteristic position when at rest.

Fig. 43. Cell stationary with flagellum coiled twice round body.

Figs. 44, 45. Individuals swimming with the flagellum and body in the position characteristic for the species when swimming; point of origin of flagellum *anterior*.

Fig. 46. Early fission stage showing second short flagellum and pseudopodium-like filament; cell with two nuclei, pyrenoid, stigma and mitochondrion dividing.

Fig. 47. Examples of different sizes and shapes of isolated starch shells; for further description see p. 284.

Fig. 48. Fission stage showing chloroplast divided.

Fig. 49. Double-fission stage producing four motile daughter-cells.

Fig. 50. Palmelloid phase with four daughter-cells.

Fig. 51. Palmelloid phase with eight daughter-cells.

Pedinomonas tuberculata (Vischer) Gams

Figs. 52, 53. Individuals with the flagellum and body in the position characteristic for the species when swimming; point of origin of flagellum *posterior*.

Fig. 54. Cell with flagellum in characteristic position when cell is at rest.

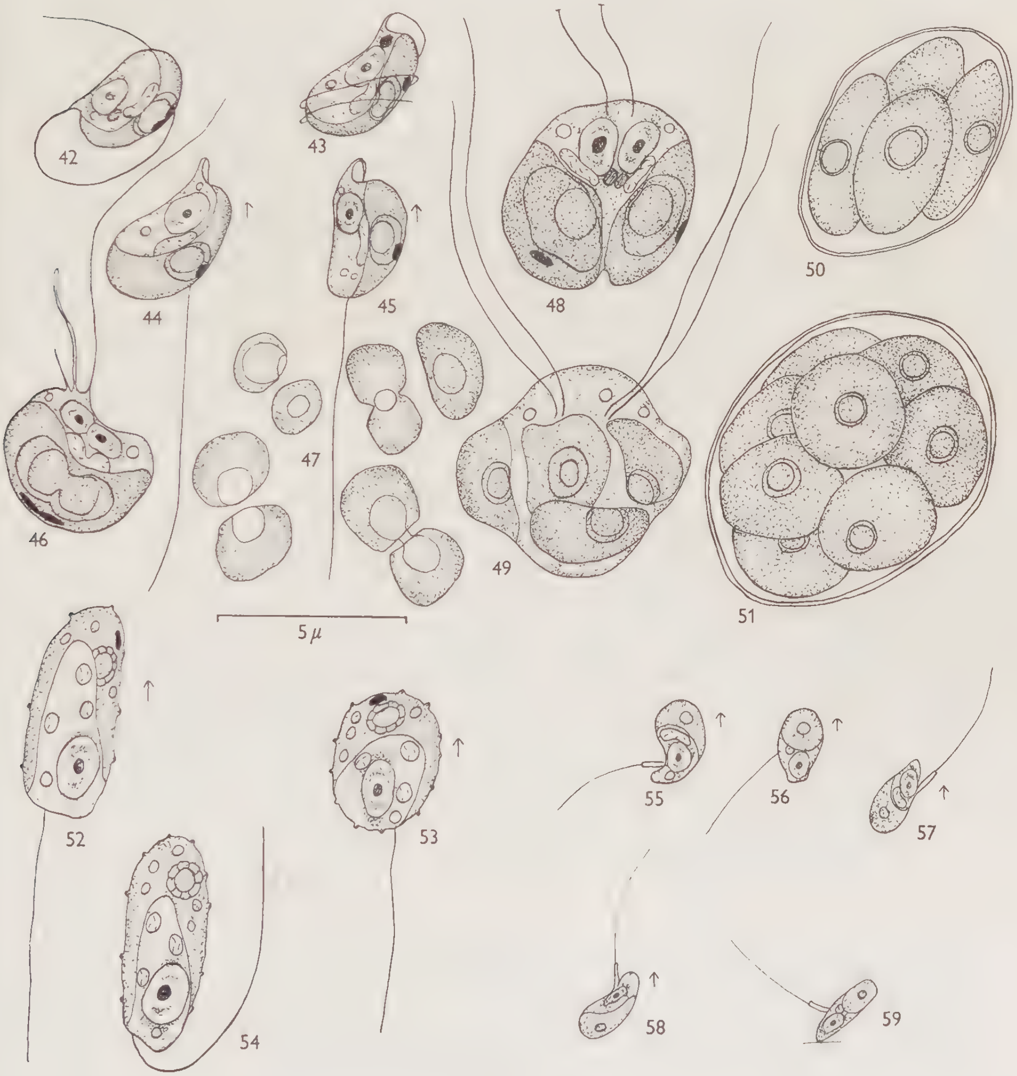
Micromonas pusilla (Butcher) comb.nov.

Figs. 55, 56. Individuals with the flagellum and body in position characteristic for the species during rapid swimming; point of origin of flagellum *lateral*.

Figs. 57, 58. Individuals swimming slowly with flagellum directed forwards.

Fig. 59. Cell attached at clear end of body; body swinging round in circles from point of attachment.

differentiated clearly from the type species of *Pedinomonas* (*P. minor*), as described by Korschikov, on the light microscopy alone. We recognize, however, that while this applies with equal force to both our species of *Micromonas*, the decision to group these together as one new genus and not as two is to some extent arbitrary, depending on our decision, on grounds of convenience, to regard the differences between these two species as less significant than the resemblances and to treat such differences as specific and not as generic criteria,



Text-figs 42–59

as explained in the introduction. The way is then clear to summarize these conclusions still further by constructing formal diagnoses for the new genus *Micromonas* and for the two species which it at present contains.

TABLE OF MORPHOLOGICAL AND ANATOMICAL CHARACTERS AVAILABLE FOR DIFFERENTIATING THE THREE SPECIES UNDER DISCUSSION FROM EACH OTHER

	Micromonas squamata	*Micromonas pusilla*	*Pedinomonas tuberculata*
Body covering	Mineralized scales over membrane	Membrane	Membrane, plus traces of calcite, cellulose, SiO_2
Flagellum:			
Attached	Anterio-lateral	Lateral	Posterior
Roots	Single	—	4 cruciform
Joined to	Nucleus	—	Chloroplast
Appendages	Scales and hairs	Terminal hair-point	2 rows fine lateral hairs
Chloroplast:			
Colour	Yellowish green	Yellowish green	Bright green
Shape	Hemispherical with pigment lamellae near outer curved surface		Curved round other protoplasmic organelles
Pyrenoid	Large uniform core of electron opaque material		Core traversed by canals
Starch	Distinct single starch shell	Starch shell minute (only visible e.m.)	Starch grains in plastid and round pyrenoid
Mitochondria	Single	Single	Several small in hollow of curved chloroplast
	Lying on surface of chloroplast		
Nucleus	Subspherical near flagellar base		Much flattened against cell surface

Diagnosis of **Micromonas** *gen.nov.*

Motile cells ellipsoid to pyriform, slightly compressed, small or very small, naked or covered with minute scales invisible with the light microscope; with one flagellum originating laterally or anteriorly but directed backwards during swimming; chloroplast single, appearing crescentic in side view with a large pyrenoid filling the concavity, starch grains absent but sometimes a starch shell round the pyrenoid staining violet (not black) with iodine; stigma present or absent; one mitochondrion lying on inner face of chloroplast; no contractile vacuole; nucleus subspherical, situated near the flagellar base to which it is sometimes attached by a delicate fibrous root. Fission in motile or palmelloid phase. Sexual reproduction not known.

Type species *Micromonas pusilla* (Butcher) comb.nov.

Diagnosis of Micromonas pusilla *(Butcher) comb.nov., emend. (Chromulina pusilla* Butcher (1952). *J. mar. biol. Ass. U.K.*, Vol. 31, p. 182.)

Motile cell pyriform, naked, 1–3 μ long × 0·7–1 μ broad. Flagellum attached laterally, less than 1 μ long, with a slender hair-point *c.* 3 μ long. Starch not detectable with the light microscope but a thin layer round the pyrenoid thought to be a narrow starch shell visible with the electron microscope. Stigma absent.

Habitat in estuaries and the open sea round the British coasts. Neo-type culture Plymouth no. 27, isolated by M. Parke from the sea at position 50° 15′ N., 04° 13′ W. (13 April 1950) at surface.

Diagnosis of **Micromonas squamata** *sp.nov.*

Motile cell ovoid with anterior pole depressed, 3–5 μ diameter; the flagellum attached anterio-laterally, 3–3·5 times cell diameter in length. Surface of cell and flagellum completely covered with slightly mineralized plate-like scales of a spider's web pattern, 0·15 to 0·4μ in diameter; a few short stout curved hairs borne laterally on the flagellum but easily detached. Single starch shell demonstrable with iodine round the pyrenoid; a small stigma sometimes present on outer face of chloroplast close to the pyrenoid.

Habitat in brackish water. Type culture Cambridge no. 1965/1, isolated by E. A. George from Brancaster Salt Marsh (salinity *c.* 15‰) in August 1951.

GENERAL DISCUSSION

Apart from the taxonomic conclusions only three general points need to be singled out for discussion. The observations on scale formation in *Micromonas squamata* constitute perhaps the most generally interesting contribution that this organism has made to botanical knowledge. Detachable surface scales are now known in great variety in pigmented micro-organisms of many groups but it is usually tacitly supposed that their place of origin is the cell surface itself, either on, in or immediately below the body membrane. Satisfactory direct evidence of mode of origin has hitherto eluded us, even in those species, notably of *Chrysochromulina* for which we have detailed electron microscopical information on the appearance and pattern of the finished scale. The observation in *Micromonas squamata* that the scales are here elaborated in the interior of the cell before being deposited on the surface individually from separate vesicles does not necessarily apply to any other flagellate. It is, nevertheless, strongly suggestive of a primitive and more plausible mechanism than any other yet suggested. It is therefore greatly to be hoped that precise observations on this particular matter may be obtainable from other genera.

Secondly, the various manifestations of hairs on the flagella on the two species described here offer many points of unusual interest. The presence of hairs as lateral appendages on certain flagella is well known in and characteristic of all the major heterokont groups (Xanthophyceae, Phaeophyceae Chrysophyceae, Saprolegniaceae, etc.) though not of the green algae as such. Nevertheless, reports claiming the presence of hairy flagella in individual genera of green flagellates have appeared in the literature more than once (e.g. Benešová, 1949; Butcher, 1959) and though these records vary very much in the degree of clarity with which the facts have been ascertained a few comparisons and contrasts can usefully be made. Thus the peculiar curved hairs encountered by us in *Micromonas squamata* bear a suggestive resemblance to hairs illustrated by one micrograph of *Chilomonas paramecium* (a colourless Cryptomonad) published by Pitelka & Schooley (1955). *C. paramecium* is described by these authors as also possessing, on the same flagellum, another type of hair more nearly comparable in morphology to those commonly known as Flimmer in some of the heterokont groups. It is therefore possible that both in this *Chilomonas* and in our *Micromonas squamata* the peculiar curved hairs represent some entirely different category of appendage from ordinary Flimmer. A comparison based on only one micrograph reproduced at a very low magnification (17,000 in Pitelka & Schooley's Pl. 22*c*) must necessarily be substantiated by fuller information before it can become more than a tentative suggestion. It would, nevertheless, be a matter of considerable interest if a real resemblance in this particular feature were to be found between two such apparently different organisms.

On the other hand, *Pedinomonas tuberculata* with its profuse garniture of very fine hairs is peculiar in several respects. The hairs here are individually far more delicate than those hitherto encountered in the heterokont groups, though in this particular character they may prove to be comparable with the Euglenoids, in some of which (e.g. *Phacus*, Manton, 1952) the hairs are also individually more delicate than average bacterial flagella. A marked difference from the Euglenoids is nevertheless provided by the presence in *Pedinomonas tuberculata* of hairs on both sides of the flagellum and also on the conspicuously posterior position of the flagellum both in point of attachment and in direction of movement. The usual position of the 'Flimmergeisel', in the heterokont types, as in the euglenoids, is forwards, even when, as in *Dictyota*, the cell may have become uniflagellate by suppression of one (the smooth) member of the pair (Manton, 1959*b*). The particular situation in *P. tuberculata* is thus at present without exact parallel.

A conclusion of some importance which these observations suggest is that outside the major heterokont groups the mere presence or absence of flagellar hairs cannot yet be used with the same precision as a phyletic guide as within the heterokont groups. Where hairy flagella are encountered among forms with chlorophycean pigments, notably chlorophyll *b*, there is reason to think that parallel evolution, possibly of more than one kind, may have taken place. If this were so, by no means all, and perhaps none, of the hairs encountered among green pigmented flagellates could be treated as homologous with those of the Phaeophyceae, Chrysophyceae, Xanthophyceae and Saprolegniaceae.

This may perhaps give point to the final comment that in very small organisms of the size range of those immediately under investigation in this communication, far greater care is necessary in formulating descriptions and in postulating phyletic affinities than has sometimes been used. The electron microscope as it can now be applied to the study of both morphology and internal structure has a uniquely important part to play in elucidating the facts regarding a region of the plant world about which very little has hitherto been known. It is of the greatest importance to clarity of thinking that hasty generalizations should not be made on insufficient evidence. If restraint is practised, however, it is to be hoped and indeed expected that when a greater number of individual taxa have been studied by comparable means some clearer general principles about how to interpret them may become available than we have at present.

Grateful thanks are due to Mr E. A. George of Cambridge for supplying the two cultures and for co-operating with information. We have to thank Dr G. Y. Kennedy of Sheffield for the pigment analyses, Miss I. Adams for assistance in the routine examination of samples and Mrs B. Hepper for testing *Micromonas pusilla* for its possible toxicity to fish. For help with the Latin diagnoses we have to thank Dr T. Christensen. We have also to thank Dr L. H. N. Cooper, Mr E. I. Butler, Mr D. Vaux and Mr A. Burd ('Sir Lancelot') for the collection of sea-water samples. Mention should also be made of the technical staffs of both Leeds and Plymouth for help in maintaining cultures, making preparations and completing the photography for publication.

SUMMARY

Pedinomonas tuberculata (Vischer) Gams has been investigated electron microscopically to the extent necessary to show that the generic name *Pedinomonas* cannot be used to include the flagellate formerly known as *Chromulina pusilla* Butcher.

A new genus, *Micromonas*, has been defined with *M. pusilla* (Butcher) comb.nov. emend. as the type species.

A second species of *Micromonas*, *M. squamata* sp.nov., has been described electron microscopically and with the light microscope. Special attention is drawn to one specific character of unusual interest, namely, the presence all over the flagellar and cell surface of an external covering of detachable plate-scales of characteristic pattern which have been shown to originate within vesicles in the body of the cell.

Attention is drawn to some of the comparative problems raised by the existence of lateral hairs of very different types on the flagellum in *Pedinomonas tuberculata* and *Micromonas squamata* respectively.

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APPENDIX

TABLE 1. RECORDED DISTRIBUTION OF *MICROMONAS PUSILLA* (BUTCHER) MANTON & PARKE

(Excluding Stations E 1 and L 2–6, September 1957–59)

Date	Position N.	Position W.	Depth (m)
12. xi. 48	50° 19·5′	04° 10′	5
8. vi. 49	50° 19·5′	04° 10′	10
29. ix. 49	50° 19·5′	04° 10′	10
14. xi. 49	50° 19·5′	04° 10′	10
8. iv. 50	49° 51′	04° 00′*	10
13. iv. 50	50° 15′	04° 13′†	0·5
9. v. 50	49° 21′	04° 54′*	0·5
30. v. 50	50° 15′	04° 13′	0·5
13. vi. 50	48° 38′	06° 20′	5
14. vi. 50	49° 19′	07° 26′	5, 10
13. ix. 50	50° 15′	04° 13′	5
29. v. 56	50° 06′	04° 21′	2
25. vi. 57	Tamar Estuary		T
16. vii. 57	50° 02′	04° 22′	0·5
6. xi. 57	Tamar Estuary		T
14. iii. 58	46° 30′	08° 00′	10, 20, 100, 500
15. iii. 58	47° 20′	07° 22′	0·5, 10, 20, 100, 200
	47° 30′	07° 18′	20, 100
16. iii. 58	47° 40′	07° 13′	0·5, 10, 20
18. iii. 58	47° 46′	07° 05′	20
16. iv. 58	46° 30′	08° 00′	127
19. iv. 58	46° 30′	08° 00′	19
20. iv. 58	47° 19′	07° 23′	9, 18, 303
20. iv. 58	47° 30′	07° 18′	10, 19
20. iv. 58	47° 38′	07° 10′	10, 225
21. iv. 58	47° 46′	07° 05′	10, 19, 125

* Samples brought in by 'Sir Lancelot'.
† Neotype strain (Plymouth no. 27) of *Micromonas pusilla* isolated from this sample.
T Townet sample.

TABLE 2 SEASONAL DISTRIBUTION OF *MICROMONAS PUSILLA* (BUTCHER) MANTON & PARKE

	International Station E 1								Plymouth Laboratory Stations				
									L 6	L 5	L 4	L 3	L 2
Depth (m)... Date	0·5	5	10	15	20	30	50	70	0·5	0·5	0·5	0·5	0·5
17. ix. 57	1	0	0	—	2	—	0	0	4	2	2	2	2
15. x. 57	0	0	0	—	0	—	0	0	0	0	0	1	0
6. xi. 57	1	—	—	—	—	—	—	—	—	—	—	—	—
3. xii. 57	4	5	5	—	2	—	3	4	2	3	3	3	4
21. i. 58	2	2	3	—	3	—	2	0	3	0	0	2	2
18. ii. 58	4	4	5	—	5	—	6	3	5	4	2	4	4
19. iii. 58	5	3	3	—	4	—	4	3	—	—	—	—	—
22. iv. 58	6	5	4	—	6	—	5	5	—	—	—	—	—
20. v. 58	3	4	4	—	5	—	4	4	6	5	4	0	3
10. vi. 58	2	5	3	6	5	—	5	6	3	3	0	0	0
9. vii. 58	6	5	5	4	6	—	6	4	4	3	1	0	0
26. viii. 58	0	0	4	—	2	3	5	4	2	0	0	2	0
1. x. 58	6	6	4	—	4	—	2	2	—	—	—	—	—
22. x. 58	6	3	6	—	4	—	3	1	3	0	0	1	0
18. xi. 58	0	—	2	—	2	—	0	0	0	0	0	0	0
13. xii. 58	1	0	0	—	0	—	0	1	—	—	—	—	—
13. i. 59	2	—	3	—	5	—	3	5	5	2	2	0	2
10. ii. 59	5	—	5	—	3	—	6	5	4	3	3	3	2
12. iii. 59	3	4	3	—	4	—	3	5	2	6	0	2	0
20. iv. 59	2	4	2	—	5	—	3	0	—	—	—	—	—
12. v. 59	4	3	5	—	5	—	1	6	5	4	2	4	4
10. vi. 59	5	3	5	—	3	5	4	3	3	4	3	1	0
11. viii. 59	5	5	4	—	6	—	5	5	6	5	5	2	3
8. ix. 59	2	3	5	2	2	—	4	4	6	3	2	0	2

6, min. no. *M. pusilla* per l.	1000
5, min. no. *M. pusilla* per l.	800
4, min. no. *M. pusilla* per l.	600
3, min. no. *M. pusilla* per l.	400
2, min. no. *M. pusilla* per l.	200
1, min. no. *M. pusilla* per l.	10
0, Absent from sample	

E 1	50° 02′ N., 04° 22′ W.
L 6	50° 06′ N., 04° 21′ W.
L 5	50° 11′ N., 04° 13′ W.
L 4	50° 15′ N., 04° 13′ W.
L 3	50° 18′ N., 04° 11′ W.
L 2	50° 20′ N., 04° 10′ W.

FORMAL DIAGNOSES IN LATIN

Micromonas gen.nov.*

Cellula erratica ellipsoïdes vel pyriformis, leniter compressa, parva vel minuta, nuda vel squamis minimis per microscopium luminarium non conspicuis induta; flagellum unicum e latere vel apice oriens, inter nandum retro deflexum; chromatophorum unicum a latere lunulare visum, pyrenoïde magno in sinu sito, amyli granulis nullis, sed testa interdum pyrenoïdi circumdata iodo violascente (non nigrescente); stigma praesens vel deficiens; mitochondrium unicum facieï cavae chromatophori appositum; vacuolum contractile nullum; nucleus subsphaericus prope basim flagelli situs, fibra subtili interdum illi conjunctus. Fissio in statu erratico vel in statu palmelloïde effecta; propagatio sexualis ignota.

Species typica *Micromonas pusilla* (Butcher) comb.nov.

Micromonas pusilla (Butcher) comb.nov., emend. (*Chromulina pusilla* Butcher (1952), *J. mar. biol. Ass. U.K.*, Vol. 31, p. 182.)

Cellula erratica pyriformis, nuda, 1–3 μ longa, 0·7–1 μ lata. Flagellum e latere oriens, vix 1 μ longum, seta tenui terminali ca. 3 μ longa auctum. Amylum per microscopium luminarium non conspicuum, sed stratum tenue pyrenoïdi circumdatum per microscopium electronicum apparens pro testa amylea exili putatum. Stigma nullum.

Habitat in aestuariis ut in ipso mari oras Britannicas alluente. Neotypus die 13 Aprilis 1950 in summo mari lat. bor. 50° 15′, long. occ. 04° 13′ lectus, in Plymouth Angliae sub numero 27 cultus, postea in vivario Cantabrigiensi depositus.

Micromonas squamata sp.nov.

Cellula erratica ovata, apice depressa, 3–5 μ diam.; flagellum ex parte anteriore lateris oriens, cellulae diametro 3–3·5plo longius. Tota cellulae ut flagelli superficies squamis araneaceïs, parce petrificatis vestita. Ciliola lateralia pauca brevia, sat crassa, curva, flagello facile adempta. Testa amylea continua pyrenoïdi circumdata iodo manifesta. Stigma parvum interdum praesens, prope pyrenoïdes facieï exteriori chromatophori appositum.

Habitat in aqua subsalsa. Typus mense Augusto 1951 prope Brancaster Angliae orientalis ab E. A. George lectus, ab eodem sub numero 1965/1 cultus, in vivario Cantabrigiensi depositus.

* The name *Micromonas* was suggested to one of us (M.P.) by Dr R. W. Butcher.

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CHEMICAL CHANGES IN SEA WATER OFF PLYMOUTH DURING 1958

By F. A. J. Armstrong and E. I. Butler
The Plymouth Laboratory

(Text-figs. 1–3)

Analyses of sea water collected during 1958 at the International Hydrographic Station E1 (lat. 50° 02′ N., long. 4° 22′ W.) are given here in the same form as in earlier reports (Armstrong, 1954, 1955, 1957, 1958; Armstrong & Butler, 1959). The methods of collection and analysis remain the same. Salinities were determined by the Government Chemist, Department of Scientific and Industrial Research. We wish again to thank Lt.-Cdr. C. A. Hoodless, D.S.C., and the crew of R.V. 'Sarsia', and Capt. W. J. Creese and the crew of R.V. 'Sula' for help at sea.

RESULTS

Temperature and salinity

The vertical distribution of temperature during the year is shown in Fig. 1. The lowest temperature measured at the surface was 8·95° C on 19 March; the highest was 16·45° C on 9 July. A weak thermocline at 15 m was established by 20 May, and it strengthened and persisted with some variation of depth down to 30 m throughout the summer. The water column had become isothermal by 22 October.

Some fluctuations of salinity occurred, as when the mean value of 35·23‰ in January dropped to 35·10 in February and returned to 35·25 in March. These changes were accompanied by the rise and fall in silicate which are shown in Table 1, and suggest a change in water mass at the station.

Phosphate

Vertical distribution is shown in Fig. 2, and integral mean concentrations in Table 1. The winter maximum found was 0·55 μg atom P/l., on 18 February. This was unusually high and in recent years was only exceeded in 1955 (0·59 in February). The lowest concentrations found were 0·07–0·09 μg atom P/l. in the top 10 m layer in June, July and August, and were about as low as are ever encountered at this station. Low values above the thermocline were recorded throughout the summer and until 1 October. By 22 October, with the autumn overturn of the water, phosphate values were uniform through the water column.

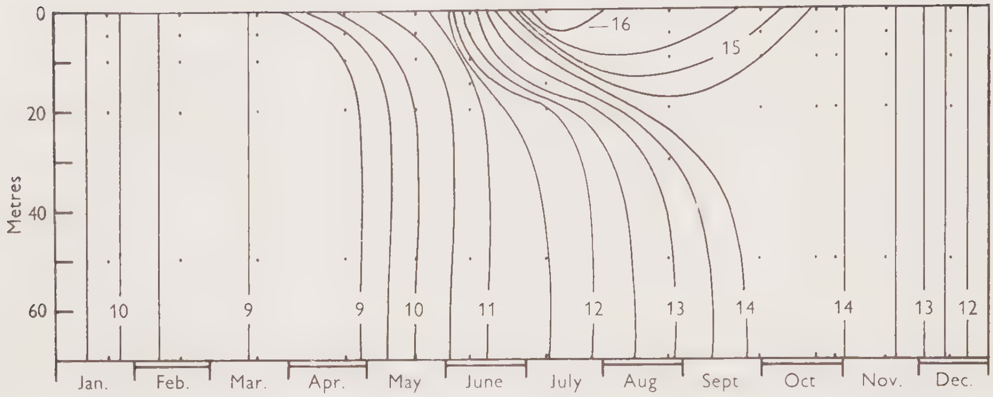

Fig. 1. Vertical temperature distribution at International Hydrographic Station E1, 1958. Contour lines at 0·5° C intervals.

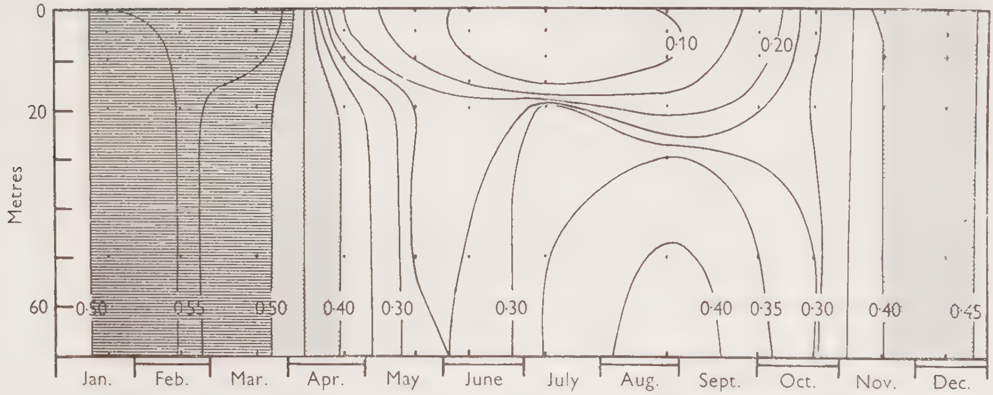

Fig. 2. Vertical distribution of phosphate at International Hydrographic Station E1, 1958. Contour lines at 0·05 μg atom P/l. intervals.

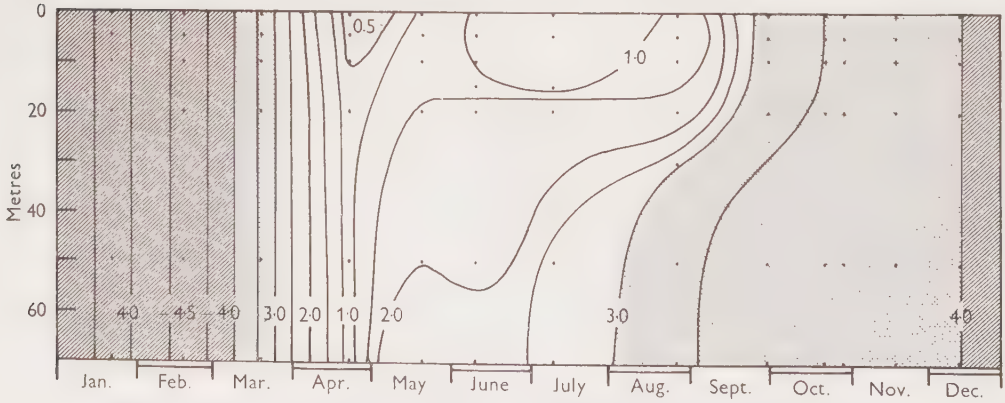

Fig. 3. Vertical distribution of silicate at International Hydrographic Station E.1, 1958. Contour lines at 0·5 μg atom Si/l. intervals.

Total phosphorus

Determinations were made in the early months of the year only, to find the winter maximum, which was 0·75 μg atom P/l. on 22 April, although sensibly similar figures were found in February and March. The value of 1·35 for the ratio of 'total' to 'inorganic' phosphorus is unusually high (Armstrong & Harvey, 1950).

Silicate

Vertical distribution is shown in Fig. 3, and integral mean concentrations in Table 1. The winter maximum value found was 4·67 μg atom Si/l. on 18 February, which was rather high. It was equalled since 1947 only in 1954 (4·70 in January) and went with the high phosphate and low salinity already mentioned.

TABLE 1. INTEGRAL MEAN CONCENTRATIONS IN WATER COLUMN AT STATION E1, 1958

Date	Phosphate (μg atom P/l.)	'Total-P' (μg atom P/l.)	Silicate (μg atom Si/l.)	Ammonia (μg atom N/l.)	Inorganic N (μg atom N/l.)
21 Jan.	0·53	0·69	3·93	—	—
18 Feb.	0·55	0·74	4·67	Less than 0·1	10·5
19 Mar.	0·54	0·73	3·64	Less than 0·1	7·6
22 Apr.	0·37	0·75	0·60	Less than 0·1	10·5
20 May	0·23	0·58	2·16	0·2	8·8
10 June	0·20	—	1·69	1·7	2·1
9 July	0·28	—	1·84	1·4	3·3
26 Aug.	0·30	—	2·61	—	—
1 Oct.	0·28	—	3·62	0·6	6·2
22 Oct.	0·30	—	3·59	—	—
18 Nov.	0·40	—	3·57	0·1	8·7
9 Dec.	0·40	—	3·95	0·2	8·9
12 Dec.	0·41	—	3·61	—	—

Low values of around 0·2 μg atom Si/l. were found in the top 10 m on 22 April, but even in the upper layers concentrations rose again in May and stayed at the 1·0 μg atom Si/l. level throughout the summer, with a temporary fall to 0·3 in July. The vertical distribution of silicate (unlike that of phosphate) had become uniform by 1 October and remained so until the end of the year.

Nitrogen

Integral mean concentrations of ammonia-N and inorganic-N (nitrate + nitrite + ammonia) are given in Table 1. The vertical distribution generally resembled that for phosphate but there are too few observations to allow a diagram to be presented. The winter maximum (of inorganic nitrogen) found was 10·5 μg atom N/l. on 18 February. The ratio N:P was then 19:1 by atoms or 8·6:1 by weight which is similar to that for 1957. On 9 July, nitrogen compounds could not be detected in the upper layers. The methods should detect 0·1 μg atom N/l., and we infer that nitrogen was the limiting nutrient for plant growth, since an appreciable quantity of phosphorus remained available. This may be the rule at this station, in recent years at least, for although we have not the necessary nitrogen analyses, it is notable that phosphate concentrations in summer have never fallen below about 0·05 μg atom P/l., and are usually appreciably higher. We estimate that the method will detect 0·02 μg atom P/l. with certainty, and it is not difficult to reduce the phosphate content of phytoplankton culture solutions below this level, if the nitrogen supply is adequate.

Nitrogen remained low in the upper layers during the summer months, became vertically uniform by 22 October, and increased thereafter until the end of the year.

Integral mean concentrations

Some figures have been discussed. The spring decreases were: phosphate 0·35 μg atom P/l., silicate 4·07 μg atom Si/l., inorganic nitrogen 8·4 μg atom N/l. The ratio N:P consumed was 24:1 by atoms or 10·8:1 by weight.

SUMMARY

The results of analysis of sea-water samples from the International Hydrographic Station E 1 during 1958 are given in graphical form and as integral mean values for the water column of 70 m. The spring decreases of nutrients, conventionally ascribed to consumption by plants were: phosphate 0·35 μg atom P/l., silicate 4·07 μg atom Si/l., inorganic nitrogen 8·4 μg atom N/l.

At the time of winter maximum of nutrients the ratio N:P was 19:1 by atoms or 8·6:1 by weight. The ratio of these elements consumed was 24:1 by atoms or 10·8:1 by weight.

The year was notable for the high phosphorus and silicon concentrations found in February.

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THE VIVIPAROUS SCYPHOMEDUSA *STYGIOMEDUSA FABULOSA* RUSSELL

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(Plates I–IV and Text-figures 1–7)

The capture of a remarkable viviparous deep-sea jellyfish, *Stygiomedusa fabulosa*, has already been reported (Russell, 1959). We have now had an opportunity of making a more detailed examination of the specimen, which has been added to the collection of the British Museum as the type specimen under the catalogue number B.M. 1960.4.7.1.

This scyphomedusa was caught in a haul with the Isaacs–Kidd net made on 18 October 1959 from R.V. 'Sarsia' with 3300 m of wire out. The net was shot at 05.53 hr in 43° 51′ N., 3° 55′ W. and reached the surface again at 12.37 h in 44° 04′ N., 3° 39′ W.

The specimen was about 50 cm in diameter across the umbrella and was not easy to handle. When it reached the laboratory it was, however, still practically intact, although it has broken into several pieces since. The form of the whole animal is shown as seen from the subumbrellar side in Pl. I. The surface of the subumbrella is smooth and it is probable that the exumbrella surface is also smooth; the latter cannot be said for certain because the whole surface of the exumbrella is deeply impressed with the outlines of the meshes of the net and most of the epidermis has been rubbed off.

The jelly is thick and firm.[1] That part of the exumbrella overlying the stomach cavity is about 25 cm in diameter and its jelly is 9 mm in thickness. The jelly of the subumbrellar floor of the stomach is about 15 mm in thickness. Beyond the margin of the stomach the jelly of the umbrella is very much thicker, reaching as much as 30 mm. This thick portion extends towards the umbrella margin for 6 or 7 cm after which the jelly again becomes thin and tapers for another 6 or 7 cm to a thin edge at the umbrella margin (Text-fig. 1 A). In the latter thin marginal region of the umbrella the jelly appears to be divided into squares in places. It seems almost certain that this is an artifact caused by the meshes of the net almost cutting through the thin jelly. The margin of the umbrella is not entire; it is much frayed and

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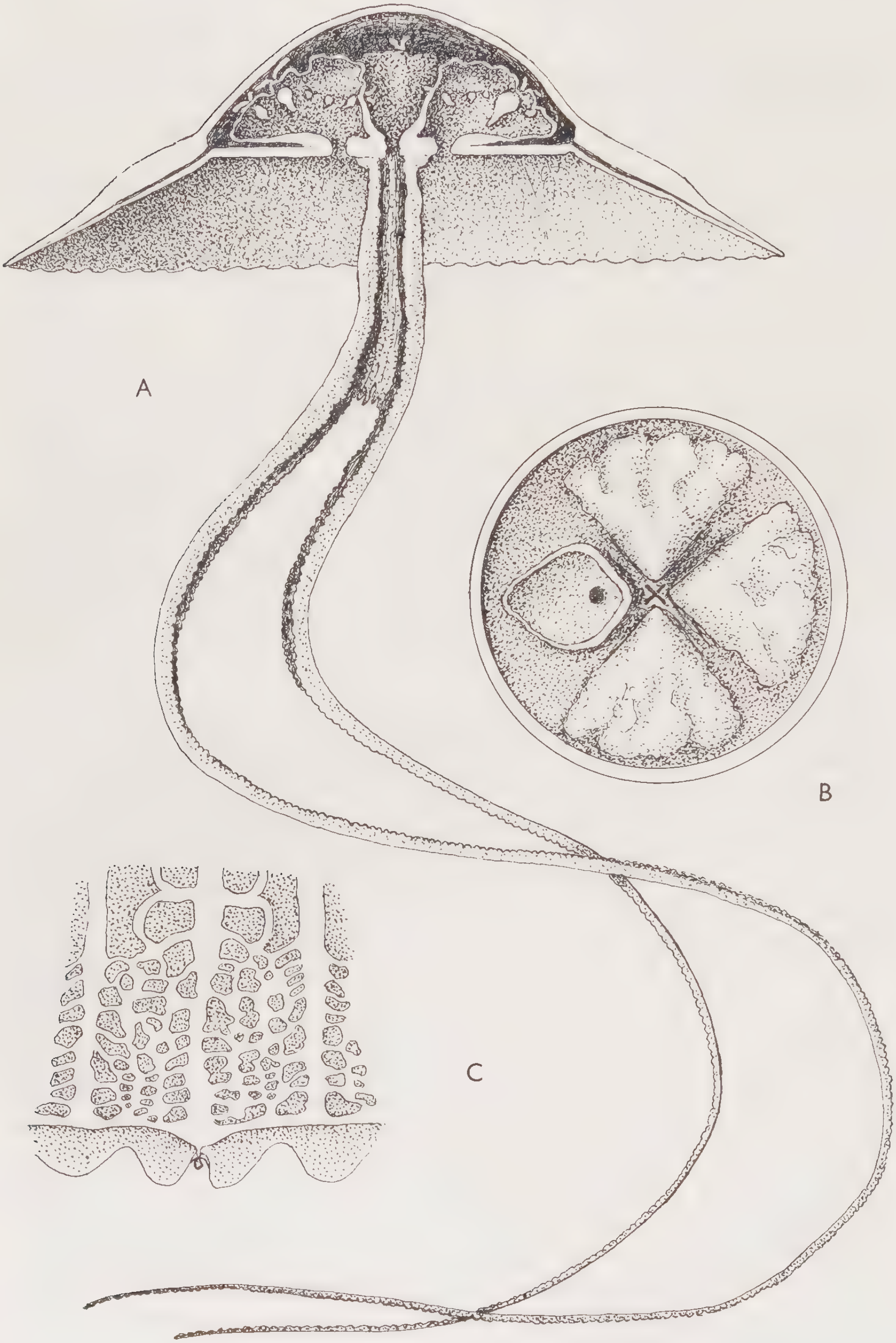
[1] When the medusa was first caught the jelly was very tough but it became brittle after being in formalin and sea water.



Text-fig. 1. *Stygiomedusa fabulosa*: A, half section of complete medusa, the two sectioned brood chambers have been pulled apart to show the one behind; B, vertical view of stomach cavity after removal of exumbrella wall to show arrangement of four brood chambers, one of which has been sectioned near its base to show subumbrellar aperture; C, tracing of enlarged photograph of portion of umbrella margin of young medusa to show gastrovascular canal system (white), marginal lappets and rhopalium. (Del. F. S. R.)

incised, and only in a few places can it be seen that it has shallow rounded lappets. As will be seen later from the description of the young medusa, it is probable that these should have been 60 in number.

There is a weakly developed subumbrellar coronal muscle in the area of the thickened jelly; the muscle fibres are striated.

In the subumbrellar wall of the stomach there are four round interradial apertures each about 15 mm in diameter and situated about 6 cm from the centre of the cross-shaped mouth opening.

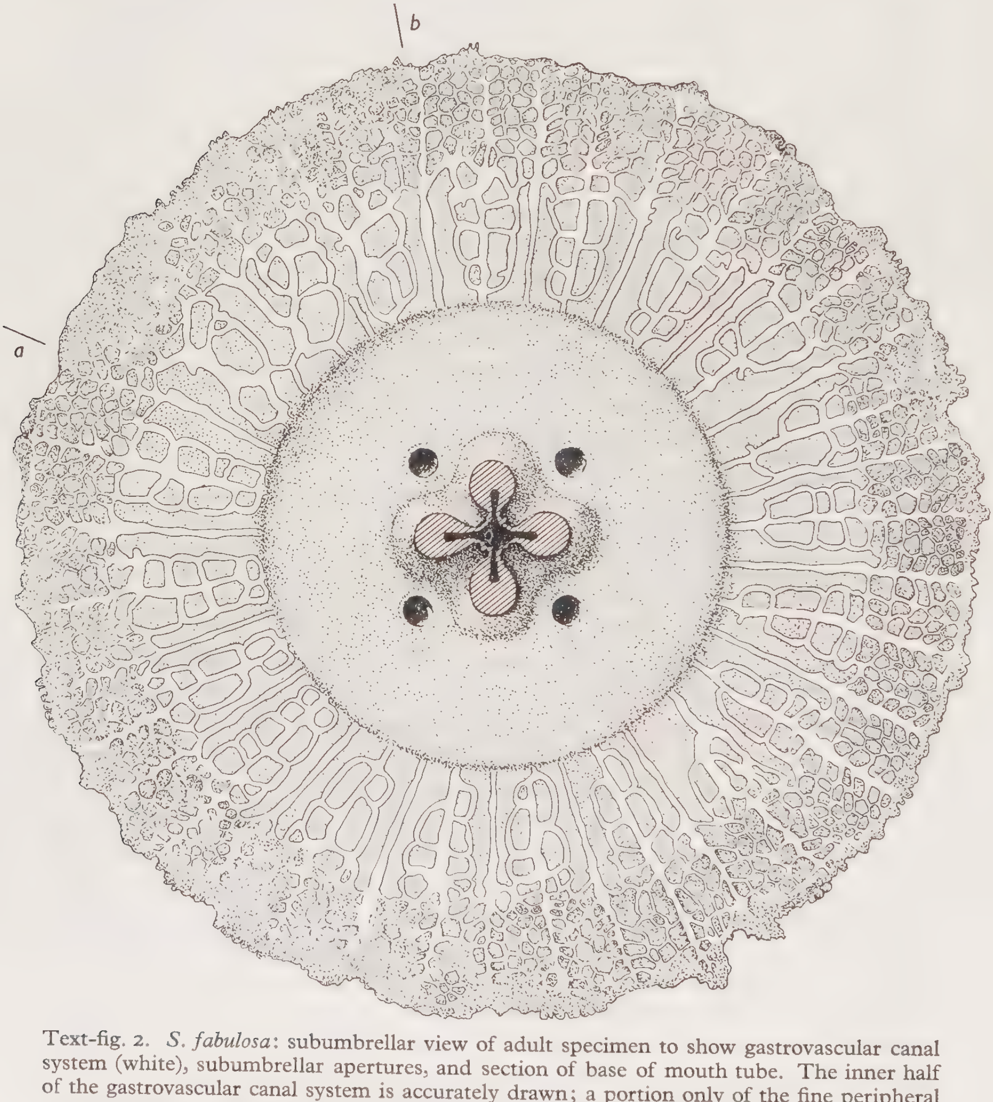
The four perradial mouth arms hang from thickened rounded bases on the subumbrellar wall. These mouth arms are each about 160 cm in length; that is, over three times the diameter of the umbrella. At their points of origin from the thickened pedicel on the subumbrella they are nearly round in section, each being about 11 cm in circumference, with a narrow longitudinal groove. Each arm soon widens out to form two flattened flanges or lips forming a deep longitudinal groove. Each mouth arm is about 4·5 cm in width where these flanges are widest a short distance below the subumbrella. The mouth arms gradually taper towards their ends. The margin of each lip is scalloped with small semicircular crenulations each about 5 mm across at its base. The ends of the mouth arms are much tattered and torn and they give the impression that they may have been branched or lobed, but this is impossible to say for certain. In any event, in this distal region the lips appear to have hollow warts.

For a length of about 15 cm a basal mouth tube is formed by filamentous frilled webs joining each arm to its neighbour.

The stomach is about 25 cm in diameter; almost all its epithelial lining is missing. Round each subumbrellar aperture thick walls of jelly rise up from the floor of the stomach (Text-fig. 1 A, B) which gradually thin out to form a brood chamber, possibly the equivalent of an enlarged subgenital pit. At this level around each brood chamber there are rows of very numerous gastric cirri, each about 5 mm in length. These cirri are typical of those of other Scyphomedusae and contain nematocysts.

Thirty-six or more oval openings round the periphery of the base of the stomach lead into a gastrovascular canal system of a distinctive pattern. In one quadrant the gastrovascular system is obviously abnormal (Text-fig. 2; Pl. I, below), but it can be concluded from examination of the young medusae that the number of openings is typically forty. Twenty of these lead into straight unbranched radial canals running towards the umbrella margin for 6 or 7 cm—that is, across the subumbrellar side of the thickened ring of the umbrella. At the point where the thick jelly thins to form the thinner peripheral portion of the umbrella these straight canals start to give off side branches and they continue to do so, giving off seven or eight branches on either side, until the straight canal enters a continuous circular canal at the subumbrella margin. The side branches themselves branch.

Alternating with these twenty straight canals and also passing across the thick part of the umbrella are twenty straight canals which give off three or four successive branches on each side, each of which re-enters the succeeding branch peripheral to it. In this way a characteristic pattern is produced having the appearance of a number of B's placed back to back. On reaching the outer periphery of the thickened part of the umbrella these canal systems



Text-fig. 2. *S. fabulosa*: subumbrellar view of adult specimen to show gastrovascular canal system (white), subumbrellar apertures, and section of base of mouth tube. The inner half of the gastrovascular canal system is accurately drawn; a portion only of the fine peripheral network of canals is exactly as in the specimen, the majority being filled in to give the general appearance. Note abnormal development between A and B. (× *c*. $\frac{1}{4}$) (Del. F. S. R.)

give rise to a finer branching system like that of the straight canals and all the branches anastomose round the outer 6 or 7 cm of the umbrella. Many of the areas enclosed by this anastomosis are roughly hexagonal in shape. The central canal of each of the 'B' systems of canals finally enters the marginal ring canal, as do some of the branches of the anastomosing system. Most of the actual margin of the umbrella is missing and the marginal ring canal can be seen in only a few places; but its continuity is confirmed by examination of the young medusa. In the zone of thick jelly the canals are about 5 mm in width.

There are apparently no marginal tentacles, and this is confirmed in the young. Only a few marginal rhopalia are present since so much of the umbrella margin is missing. These appear to be small simple statocysts whose stalks receive canals from the ring canal. The rhopalia, on the basis of the young medusa, are twenty in number and are situated at the ends of the 'B' systems of canals, so that these can now be called rhopalar canals as opposed to the unbranched inter-rhopalar canals.

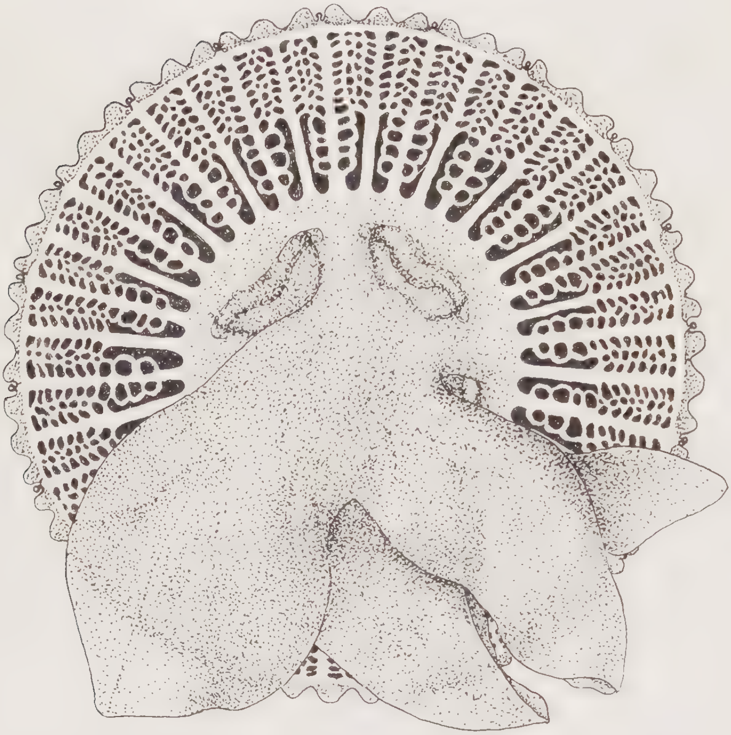
The whole medusa when freshly caught was a deep brown red or plum colour typical of deep-sea animals. Against this coloration on the subumbrella side the opaque white epithelium of the gastrovascular canals shows up clearly and makes a distinctive pattern. The coloration which extends right through the jelly is due to large numbers of spherical cells embedded in the mesogloea. Each of these cells has a large nucleus and on one side a mass of pigment granules near which is a mass of smaller refringent granules. Near the surface of the umbrella there is a thin layer of pigment granules in the mesogloea itself just beneath the surface epithelium.

The colour leaches out, making formalin and sea water pink in colour. Dr G. Y. Kennedy kindly examined the pigment for us, and finds that the bulk of it is a melanin.

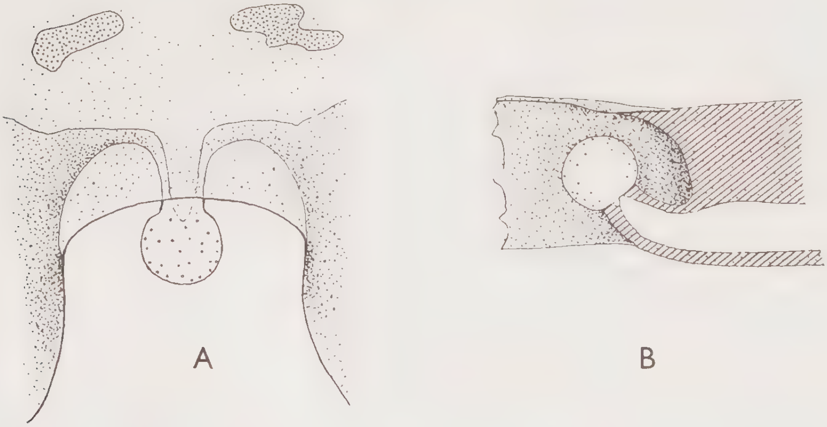
The young medusa

Two perfect specimens of young medusae were found at the bottom of the bath in which the adult was brought ashore. The stomach wall of the parent was already broken open, and it is probable that in turning the specimen over these young medusae fell out into the surrounding medium. One specimen was slightly larger than the other, their diameters being 9·6 and 8·5 cm respectively.

These young medusae are perfect miniatures of the adult in most respects (Text-fig. 3; Pl. III). The jelly is, however, still very thin and membranous and tends to curl inwards at the margins. In each specimen there is a hole about 2 cm in diameter on the exumbrella side over the stomach, presumably where the medusa has broken away from its embryonic attachment, probably prematurely. When lying flat in a dish with the subumbrellar side downwards and drained of surrounding fluid the exumbrella surface shows clearly round



Text-fig. 3. *S. fabulosa*: drawing of young medusa; the gastrovascular system has been drawn semidiagrammatically to indicate the basic pattern. (Nat. size.) (Del. F. S. R.)



Text-fig. 4. *S. fabulosa*: rhopalium of young medusa: A, exumbrellar view; B, semidiagrammatic lateral view half sectioned to show rhopalar canal; the statocyst is not sectioned. (Del. F. S. R.)

its outer half forty radiating ridges corresponding to the septa which lie between the forty main canals of the gastrovascular system. The margin of the umbrella has sixty evenly-rounded lappets and twenty marginal rhopalia. The bases of the two lappets which lie one on each side of a rhopalium together amount to about 8 mm. Between each pair of rhopalar lappets is a single lappet which is situated opposite the end of an inter-rhopalar canal and has a base about 5 mm long. The radial length of each type of lappet is about 3·5 mm. Thus there are forty rhopalar lappets and twenty inter-rhopalar lappets. In the smaller of the two specimens the lappets have not developed to the stage at which they are completely separated to their bases.

The diameter of the stomach is approximately half that of the umbrella. From it radiate forty canals separated by forty clearly seen septa. The gastrovascular canal system is developed exactly as in the adult; there are twenty rhopalar 'B' canals and twenty inter-rhopalar unbranched canals and all run into a complete marginal ring canal after branching to form the peripheral anastomosis of canals.

The mouth arms are very membranous and not yet formed like those of the adult. Their length is not quite as much as the diameter of the umbrella. They are very broad and leaf-shaped, and joined to form a circular basal mouth tube for about half their length.

At the point of origin of each mouth arm from the subumbrella surface the jelly is thickened and this stronger jelly runs radially to the outer margin of the stomach. Between these stiffened areas the subumbrellar wall of the stomach is still very thin and the brood chambers which are already forming push this thin jelly outwards as do the gonads in *Pelagia*. Presumably as the medusa grows the jelly of the stomach wall increases in thickness until only the subumbrellar apertures are left; the condition in *Stygiomedusa* approximates to that indicated by Agassiz & Mayer (1898, plate. viii, fig. 14; pl. x, fig. 23) for *Dactylometra*.

While in external appearance the walls of developing brood chambers give the impression that they might be similar to the gonads of *Pelagia*, a microscopic examination shows no obvious signs of sexual cells. The chamber has a wall of mesogloea from which tapering projections of mesogloea run towards the centre and themselves give rise to branches. The lining epithelium consists mainly of columnar cells, and interspersed at regular intervals are round cells with larger granules, and there are also nematocysts in various stages of development.

There are no marginal tentacles. There are twenty rhopalia, each consisting of a simple statocyst with a short canal entering its stalk from the ring canal. The rhopalia are colourless except for a few scattered pigment cells. The bases of the adjacent marginal lappets join to form a roof over the rhopalium which is itself directed upwards (Text-fig. 4).

The colour of the young medusae is brownish-red, and this coloration extends right through the mesogloea, as in the adult, and is due to numerous spherical cells containing pigment granules. As in the adult also the opaque whitish epithelium of the gastro-vascular system shows up its pattern, and there is also an opaque white line along the axis of each mouth arm.

Reproduction

The four brood chambers protruding into the stomach cavity are covered on the gastric side in this preserved specimen by an epithelium which is folded into narrow ridges. This epithelium consists of columnar cells with nematocysts scattered among them. Around the lower periphery of the brood chamber is a raised convoluted frill along the folds of which the gastric cirri are distributed. The whole forms a band about 20 mm high.

A little above this band, running along the side walls of the brood chamber, is a stripe of modified epithelium which may be called the germinal line (Pl. II, below), as it is from its tissue that the remarkable reproductive bodies develop. In our specimen a whole range of developmental stages can be found.

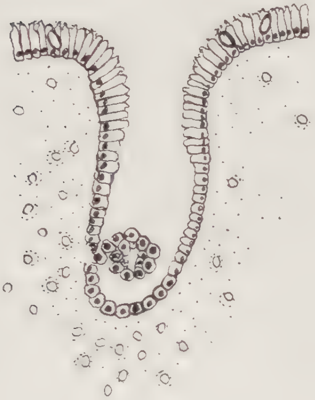
The germinal line forms a shallow groove whose epithelial cells differ from those of the surrounding columnar epithelium in being more cubical and having large rounded nuclei. The cells in the mesogloea beneath are also more numerous than elsewhere. In many places along the line there are small pits in which the cells often show an irregular arrangement. The multiplication of the epithelial cells in some of these pits produces deeper invaginations which are evidently the first stage of the processes leading to the development of the future young medusa. Text-fig. 5 shows a section of such an invagination in which there is a small clump of cells forming a vesicle, presumably the first formation of a cyst. No sexual cells could be found.

The cyst grows into an oval body with a more pointed end on the subumbrellar side. As this increases in size it pushes out the wall of the brood chamber so that it projects into the cavity of the chamber. At the same time at the opposite end of the cyst two outgrowths develop which run horizontally in opposite directions so that the cyst now appears T-shaped (Text-fig. 7B). At the stage when the cyst is 8–11 mm in length the tubular outgrowths run along the gastric surface of the chamber wall for 8–10 mm; the outgrowths are 2·0–2·5 mm in width.

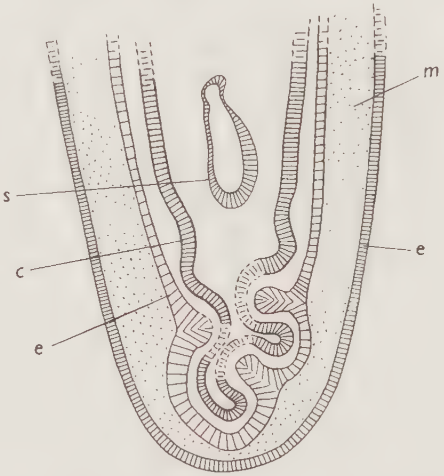
The cyst, continuing to increase in size and protruding farther into the cavity of the brood chamber, carries with it the enveloping brood chamber wall, which becomes more and more attenuated until it forms a thin membrane or capsule surrounding the cyst. At the same time the tubular outgrowths at its base grow away from the gastric wall of the chamber so that they project freely into the stomach (Text-fig. 7C).

At an early stage another body is developing within the cyst. This body we call the scyphistoma and from it a single medusa develops. From this stage onwards the cyst wall can be regarded as a chorion.

The capsule and its contents, from the outside inwards, thus consist of (*a*) an outer wall which is the modified wall of the brood chamber, consisting of two epithelial layers, ectodermal and endodermal in origin, with a thin mesogloea between them; (*b*) the cyst or chorion which consists of a single layer of tall columnar cells with an inner underlying basal membrane; these cells, presumably absorptive and secretory in function, have projections on their free margins and contain very numerous granules; and (*c*) the wall of the scyphistoma which in later stages consists of two layers of epithelium with a thin layer (? mesogloea) between them.



Text-fig. 5



Text-fig. 6

Text-fig. 5. *S. fabulosa*: section through depression on germinal line containing developing cyst. (Del. F. S. R.)

Text-fig. 6. *S. fabulosa*: diagram of longitudinal section of distal end of small capsule 8 mm long. Note the pocketed area and the young scyphistoma lying free in the cavity of the cyst. *c*, cyst; *e*, parent epithelium; *m*, mesogloea; *s*, scyphistoma. (Del. W. J. R.)

Measurements of some of the smaller and medium-sized capsules are given in Table 1.

TABLE 1. SIZE OF CAPSULES

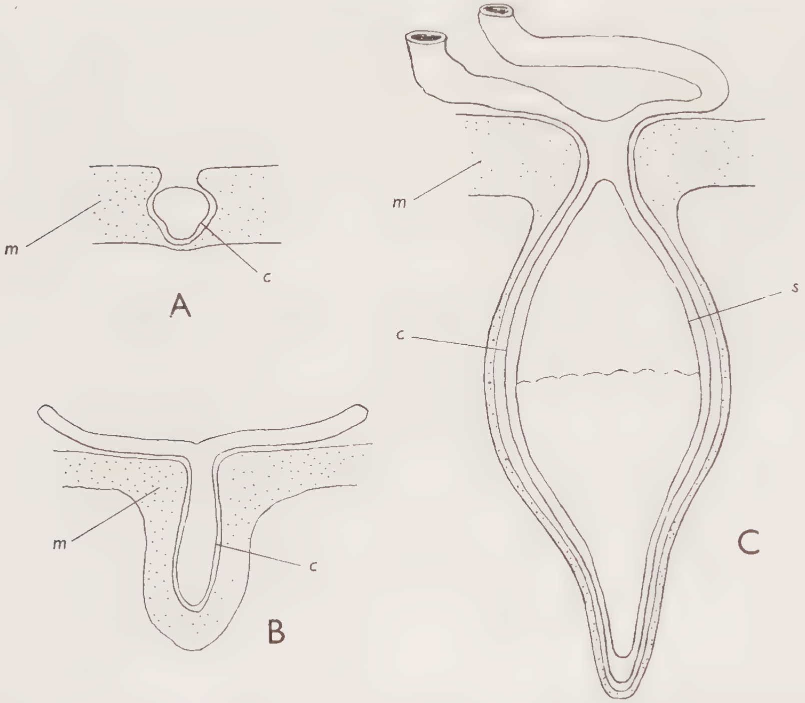
Dimensions of smaller and medium-sized capsules, projecting from the subumbrellar wall of the chamber illustrated on Pl. II (below). The measurements do not include parts embedded in the subumbrellar wall or projecting into the stomach.

	Measurements in mm							
Total length of subumbrellar surface of chamber	8·0	8·4	8·6	10·3	31·5	37·6	38·6	45·4
Maximum diameter	3·0	3·0	2·4	4·0	12·0	17·6	17·8	21·3

The larger capsules over 10 mm in length are pinkish-white in colour and become oval in shape with their distal ends narrowing rather suddenly; they are thus somewhat teat-shaped, and their tips are often brown in colour.

The size of a cyst just before it begins to push out the chamber wall is 2·6 mm long and 2·0–2·3 mm in diameter.

The basal outgrowths of the cysts are hollow tubes, closed at their distal ends. They may reach a length of 20 cm, and lengths of 12–17 cm were common. Only the smaller outgrowths up to 3 cm in length are still attached and complete in our specimen. All the others were broken off near the chamber wall and found floating loose in the fluid surrounding the medusa in its container.



Text-fig. 7. *S. fabulosa.* Diagrams of various stages of development of capsules. A, cyst about 2 mm long; B, showing early development of tubular outgrowths at base of cyst; C, fully formed capsule (the ends of the tubular outgrowths are shown as cut off). *c*, cyst or chorion; *m*, mesogloea; *s*, scyphistoma. (Del. F. S. R.)

These tubes have an outer layer of high columnar epithelium the cells of which have numerous granules and projections on their free margins, similar to those of the part of the chorion within the capsule. This is yellowish to orange in colour in the newly captured medusa, and in many instances the epithelium had become stripped from its basal membrane.

Inside some of the small tubes were seen many free, scattered, rounded cells some of which were in process of division. In larger tubes there were, lying free, rounded masses of cells resembling morulae, blastulae and planulae.

In the capsular portion of the chorion differentiation and formation of the scyphistoma begins at an early stage. At a capsule length of 8 mm sections revealed that the inner epithelium of the capsule wall, namely parent tissue, was much developed and pocketed in the distal tip of the capsule and that the chorion tissue was continuous in the pockets and followed their contours (Text-fig. 6). Preservation of the tissue for histological examination was, however, not at all good. Within the chorion sac, lying free in the cavity, there was a young scyphistoma 0·35 mm long. As the scyphistoma increases in size it takes the general shape of the capsule, the distal narrowed end being the developing mouth arms. Although in many of the larger capsules preservation was poor, it was possible to see the umbrella margin and the indications of a gastrovascular canal system in process of formation; but on dissection many of these disintegrated. The most developed capsule, 6·5 cm long and 4·3 cm wide, contained an almost fully developed medusa (Pl. II) complete with gastrovascular system, and mouth arms and the reddish purple coloration typical of the adult.

Some of the capsules had subsidiary capsules developing at their bases (Pl. IV, above).

In some of the capsules differentiation appears to have been abnormal and budding abortive. This feature may be linked with the four abnormal young medusae found (Russell, 1959). In these the medusa had the normal pigmentation but was flattened and pancake-shaped (Pl. IV, below). There were no mouth arms and no stomach, the digestive system being represented by a series of reticulate canals converging on a central point where the mouth should have been.

There remains the question, how does the young medusa escape from the brood chamber? Although the circular subumbrellar aperture connecting the chamber with the exterior is small (15 mm in diameter), it is possible that the young medusa, which is very plastic, might squeeze through. It should, however, be remarked that the only capsule with a very well-developed young medusa in it, although still attached to the subumbrellar wall of the brood chamber, is sticking through an opening in the wall into the gastric cavity so that the young medusa could escape through the mouth. As a few other smaller capsules had also passed through obvious tears in the wall this may not have been natural.

The excised brood chamber shown in Pl. II (below) has ten or so capsules visible to the naked eye. One cannot say how many more very small developing cysts are present. But it is evident that production of medusae is a continuous process and that the number produced by one parent medusa must be at least 50 and may be 100 or more.

Systematic position

In its structural characters *Stygiomedusa* is obviously quite a typical semaeostome scyphomedusa. In its general form and the arrangement of its gastrovascular canal system it agrees with the Ulmaridae, and it differs structurally from them only in the absence of marginal tentacles. We think that the family characters of the Ulmaridae should be enlarged to include species without marginal tentacles and that within the family there should be a new subfamily, the Stygiomedusinae of which *Stygiomedusa* would be the type genus.

DISCUSSION

Stygiomedusa fabulosa is the largest deep-water medusa known; its reddish purple colour and its viviparity are characteristics shared with many other animals living in very deep water. However, viviparity in which a few large medusae with adult characters are produced was hitherto quite unknown in the Scyphomedusae and the brood-caring mechanism by which it is achieved is unique in the history of the Cnidaria.

The brood-caring habit in its various forms is found in many benthic and bathypelagic forms and has been noted for many groups including crinoids (John, 1938), the pelagic octopod *Vitreledonella* (Joubin, 1929, p. 18) and in many gastropods (Thorson, 1950). In many species this is accomplished by the inclusion of many eggs within the single capsule and the successful ones emerge as miniature adults at the expense of the remaining eggs which are usually termed nurse cells.

In *Stygiomedusa* there are no nurse cells, nor have any sexual cells been seen; the uniqueness of its viviparity when compared with the usual methods of brood-caring will be appreciated when it is noted that it is the result of the telescoping of the metagenesis which we find in many Cnidaria and its adaptation for nursing the young medusa.

When we consider the life cycle of a common coastal Ulmarid medusa we find that it has the type of life cycle known to us in the common jellyfish *Aurelia aurita* L. Here the fertilized eggs develop into free-swimming planulae and then into polyps or scyphistomae anchored to suitable substrata in the sublittoral zone; these in turn may reproduce themselves asexually by budding or by the formation of podocysts before transforming themselves into strobilae budding off a large number of ephyrae or larval medusae. These feed on other planktonic organisms and finally acquire the characteristics of the adult. Encystment of the planula also takes place in some scyphomedusae (Rees, 1957*a*, p. 483), although this fact is seldom mentioned in text-books: the encysted stage, which is of variable duration, gives rise to a young scyphistoma.

In a scyphomedusa which has acquired a deep-water habit, continuation of this type of life cycle involving a benthic polyp stage is beset with difficulties.

Even if a suitable substratum could be found, food would probably be scarce both for strobilation and for the growth of the young medusa. The pelagic surface jellyfish *Pelagia perla* (Slabber) has solved this difficulty by having a more direct development in which a single egg gives rise to a single adult and it seems probable that this is what happens also in the bathypelagic medusae *Atolla* and *Periphylla*.

The hydromedusa *Bougainvillia platygaster* Haeckel is in process of becoming an oceanic species and has partly solved the difficulty of finding a suitable substratum by asexual propagation of the life cycle (Kramp, 1957; Rees, 1957*b*). In this species, the immature germinal tissue gives rise directly to stolons or polyps, which, in turn, bud off medusae. Similar phenomona, although differing in detail, have been noted in *Proboscidactyla ornata* and *Phialidium mccradyi*. Thus the familiar pattern of alternation of polyp and medusa may result either from sexual or (more rarely) asexual reproduction of the polyp phase.

Bearing this in mind, we have to consider whether *Stygiomedusa* has acquired an entirely new method of reproduction or whether the familiar Ulmarid type of life cycle has been highly modified to suit the needs of a brood-caring deep-sea species.

The cyst is produced, as has been noted, by asexual budding of parent germinal tissue and this process was hitherto not known to take place in Scyphomedusae. Apart from this, however, the life cycle is clearly a telescoped and much modified Ulmarid pattern. The germinal tissue as already noted forms a stripe of modified epithelium, and it is not possible to decide, from the single medusa available to us, whether this tissue is rudimentary or regressed, or even whether sexual reproduction also may or may not take place at some stage in the life of the medusa. In *Bougainvillia platygaster*, where a parallel case of asexual propagation is known, Kramp (1957) emphasized that 'all the specimens were immature'.

The asexually produced cysts lie in endodermal pockets in the roof of the brood chamber and are analogous with the podocysts of *Chrysaora* and *Cyanea* that may arise either from fertilized eggs or asexually from the bases of scyphistomae. In podocysts of *Chrysaora* and *Cyanea* the contents become organized within the cyst to form ectoderm and endoderm separated by mesogloea so that when the polyp emerges it quickly assumes the form of a scyphistoma. It appears likely that this preliminary differentiation into tissues also takes place in *Stygiomedusa*, but so far as we are aware no obvious primary polyp is formed.

The body within the cyst or chorion sac, which we regard as an atentacular scyphistoma and which is present when the capsule is less than 8 mm in length, results in the budding of a single medusa. This type of monodisk strobilation is also found in the rhizostome medusa *Cotylorhiza tuberculata* (Claus, 1892). The young medusae retain their connexion with the central lumen of their scyphistomae until almost fully formed, and those with a hole in the top of the umbrella found floating freely in the container (see p. 307) had obviously been torn out of their capsules before they were quite ready for liberation.

It is considered that the abnormal medusae found in this species represent some accident or failure in the normal course of development.

Some shallow-water Scyphomedusae protect their young until the planula stage; in *Aurelia* the fertilized eggs are 'retained in small pouches near margins of the free edges of mouth-arms and finally set free in the planula stage' (Mayer, 1910, p. 625). *Cyanea* behaves similarly but nothing more elaborate than this was known, so that *Stygiomedusa* is unique in the complexity of its brood-caring mechanism.

Many deep-water organisms are thought to have been evolved by migration from shallow or surface water, and *Stygiomedusa* is probably no exception. Encystment of the larvae, such as frequently occurs in *Chrysaora* and *Cyanea*, was probably a major factor in enabling the life cycle to take place in the parent medusa. In this way the jellyfish became independent of a substratum for its polypoid phase.

To sum up, the uniqueness of the reproduction of *Stygiomedusa* will be appreciated from the fact that the cyst wall acts as a chorion for the scyphistoma and draws its nourishment directly from the lumen of the parent by means of its tube-like projections.

Our grateful thanks are due especially to Dr J. S. Alexandrowicz who has prepared many sections and helped us considerably in the interpretation of the process of development of the young medusa. We would like also to thank Mrs E. A. Peace for the photographs in Pls. I, II and III, Mr P. J. Green for those in Pl. IV, and Lt.-Cdr. C. A. Hoodless and the crew of R.V. 'Sarsia' for their care in bringing the medusa safely to Plymouth.

SUMMARY

A description is given of the deep-sea scyphomedusa *Stygiomedusa fabulosa* Russell. In general structure this is a typical semaeostome medusa except that it has no marginal tentacles. It is 50 cm in diameter and has the deep reddish colour typical of a deep-sea medusa, due to a melanin.

The medusa is remarkable in that it has an unusual method of asexual reproduction and is viviparous. The young medusae are developed in capsules projecting into the cavities of four brood chambers which protrude into the stomach.

Special cells along a germinal line of the endodermal epithelium of the brood pouch give rise to cysts which have tubular outgrowths into the stomach cavity. Each cyst produces a simple sac lying within it which may be

regarded as a scyphistoma giving rise to a single medusa. The cyst then acts as a chorion passing nourishment to the developing medusa.

The significance of this method of reproduction is discussed.

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EXPLANATION OF PLATES I–IV

Plate I

Stygiomedusa fabulosa. Above, complete specimen; there is a metre rule in front of it. *Below*, portion of umbrella margin to show pattern of gastrovascular canal system; the central section is abnormal. A bit of the brood chamber and capsular tissue is projecting through the subumbrellar aperture.

Plate II

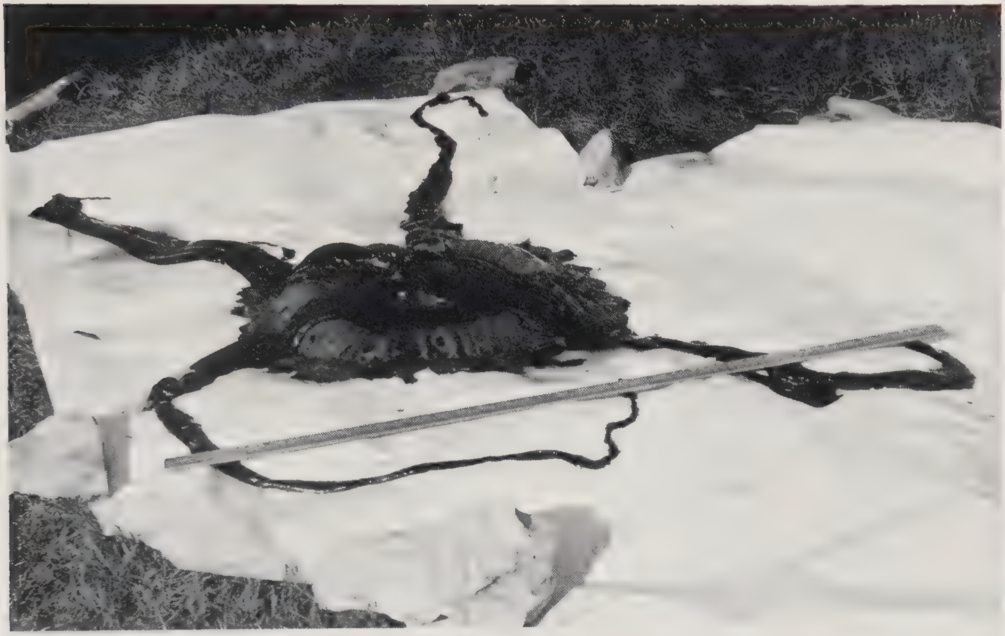
S. fabulosa. Above, the four brood chambers seen from above after removal of the exumbrellar wall of the stomach. In the right-hand top corner there is a capsule containing a nearly fully developed young medusa; this and a few other capsules are protruding into the gastric cavity through openings or tears in the wall of the brood chamber. *Below*, an excised brood chamber seen from the subumbrellar side: the capsule with the young medusa can be seen projecting beyond the centre of the lower margin. The arrow points to the germinal line.

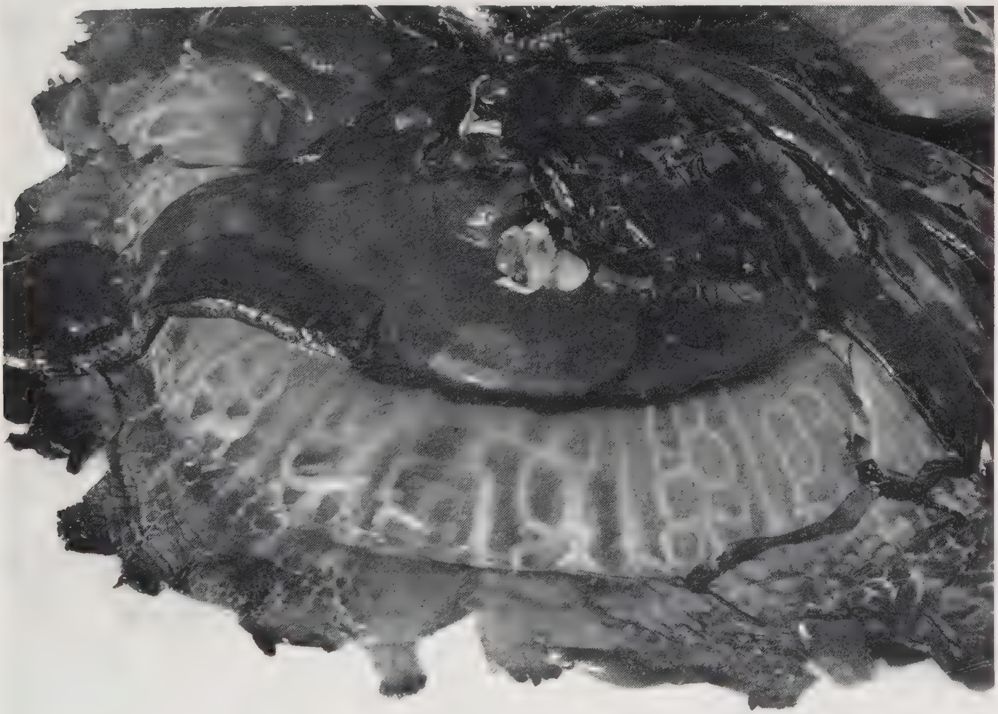
Plate III

S. fabulosa: two views of one of the young medusae. In the lower photograph a developing brood chamber can be seen at the base of the right-hand mouth arm. (*Ca.* nat. size).

Plate IV

S. fabulosa. Above, enlarged photograph of capsule to show subsidiary capsule at its base. *Below*, abnormal young viewed by transmitted light; the specimen is torn.





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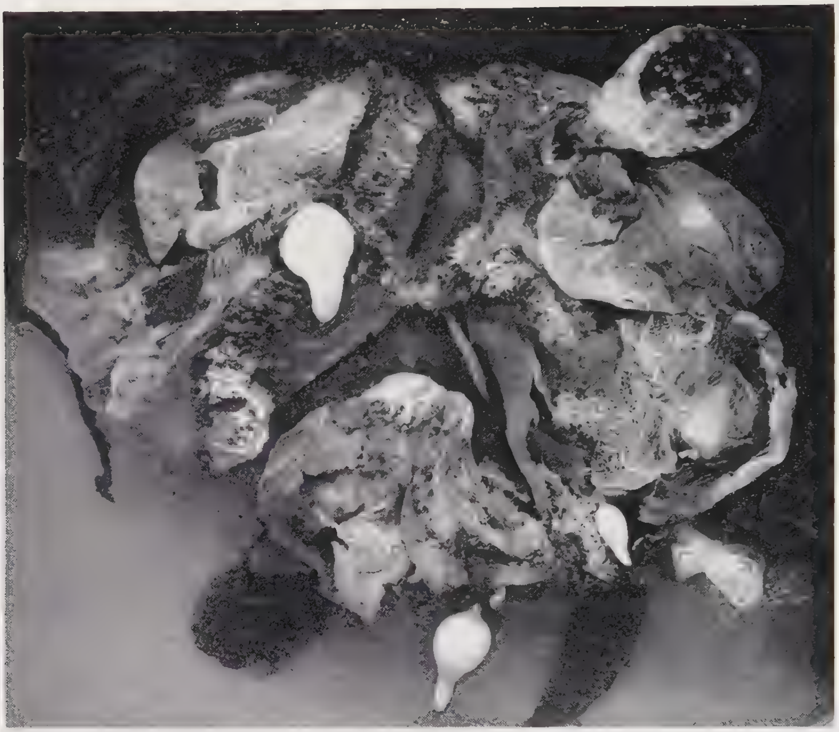

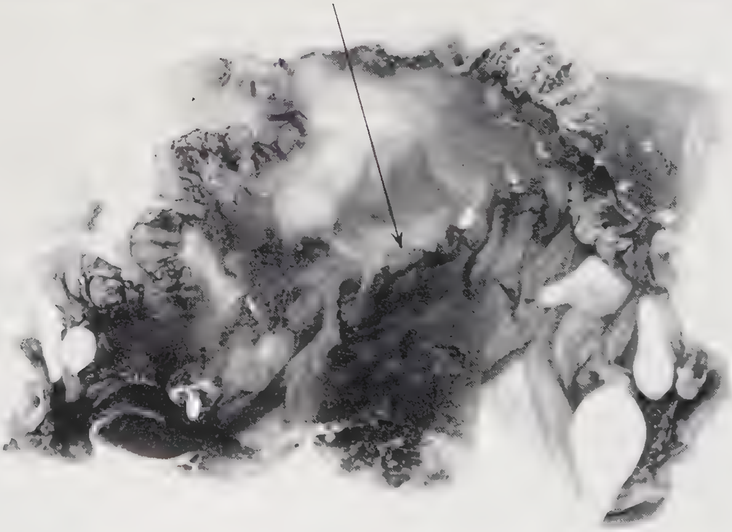

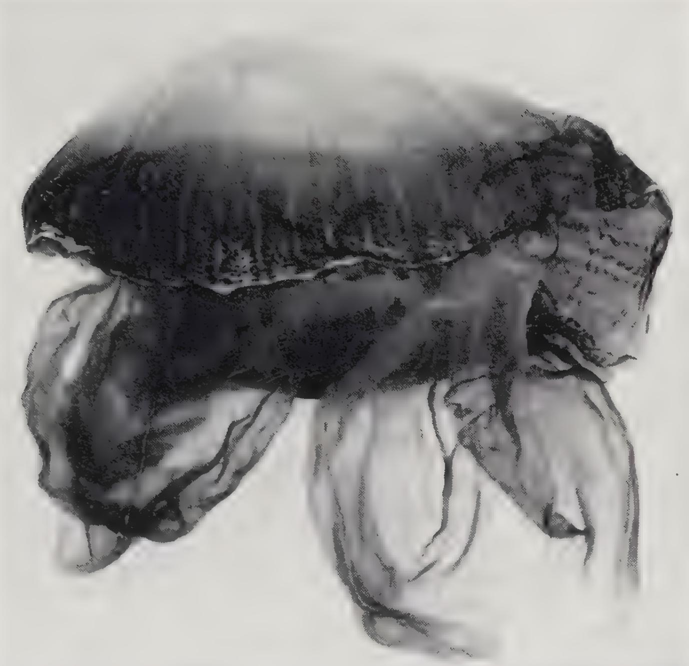

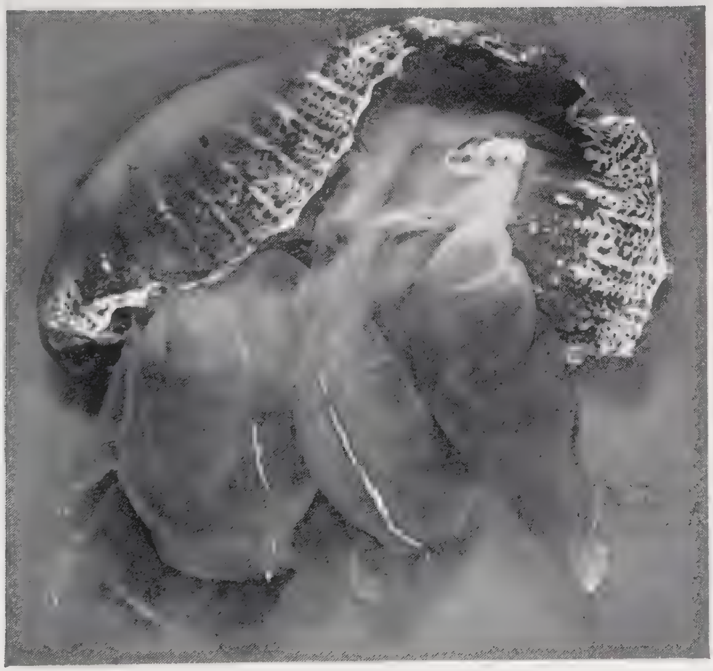

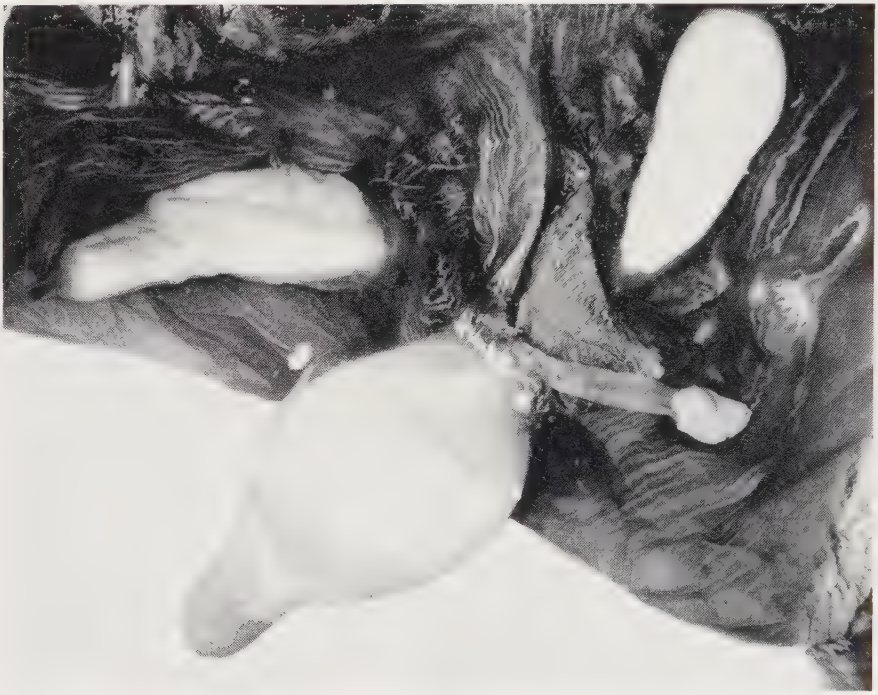

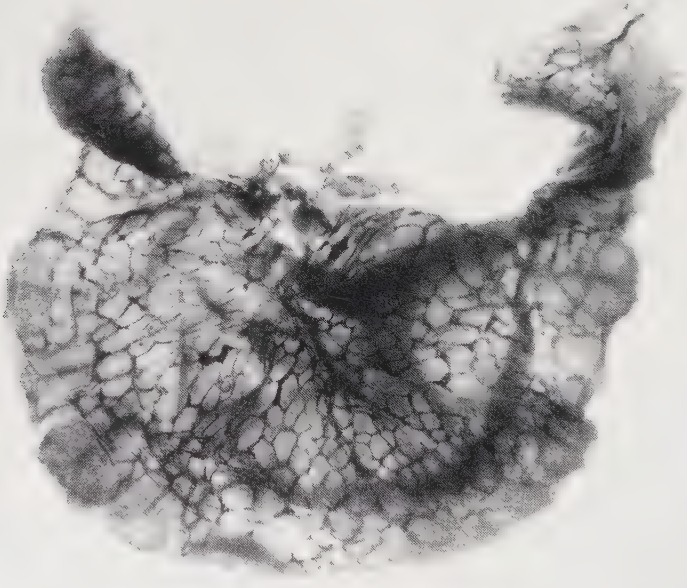

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THE OCCURRENCE OF *INGOLFIELLA* IN THE EDDYSTONE SHELL GRAVEL, WITH DESCRIPTION OF A NEW SPECIES

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(With Text-figs. 1–5)

Among the various small Malacostraca that have lately been found living interstitially in the Eddystone shell gravel (see Spooner, 1959*a*, *b*), one of the more remarkable is a new member of the genus *Ingolfiella*. This genus of small colourless blind amphipods occupies a very isolated position, and is customarily given the rank of a separate suborder. The six species hitherto recognized are listed in Table 1, and their geographic relationships shown in Fig. 5 (p. 328).

TABLE 1. OCCURRENCE OF INGOLFIELLIDS

			Habitat			
Species	Reference	Geographical area	Depth or height	Substratum	No. of specimens examined	Size (length, mm)
Ingolfiella abyssi	Hansen (1903)	North Atlantic, Davis Strait	1870 fm (3420 m)	Globigerina clay	1	2·5
I. littoralis	Hansen (1903)	Gulf of Siam	1 fm (2 m)	Coral sand	1	1·5
I. acherontis	Karaman (1933), Hertzog (1935), Karaman (1954)	Jugoslavia, Skoplje	*c.* 250 m†	Subterranean ground-water	1*	2·5
I. leleupi	Ruffo (1950, 1951)	Belgian Congo, south-east	Above 1000 m†	Cave pools	44	12·5–14·5
I. petkovskii	Karaman (1957)	S. Jugoslavia, at foot of Macedonian mountains	*c.* 50 m†	Subterranean ground-water	Several	Up to 2·0
I. ruffoi	Siewing (1958)	Peru, open coast	Intertidal	Interstices of shingle	100+	1·12–1·52

* Karaman (1957) mentions more recent additional material. This has not been reported on yet.
† Above sea-level.

Of the six species, three were found in marine and three in freshwater habitats. The geographical range could scarcely be more diverse, since it includes abyssal ocean floor (and so a site that was presumably never part of a continent) and uplands on a continental shield (that may never have been under the sea), while the substratum includes both Globigerina ooze settled in quiet oceanic depths[1] and shingle of a wave-beaten shore. The temperature range, as Siewing (1958) has pointed out, is also very wide.

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[1] A detailed analysis of the bottom on which *Ingolfiella abyssi* occurred is given by Boeggild (1900).

The seventh species now to be described has been isolated from two samples of the shell gravel collected with the Forster anchor dredge, at about 25 fm, about 1 mile north-westward of the Eddystone Rock. One sample, collected on 31 March 1959 and cursorily examined, produced two specimens; and another, collected on 9 September 1959, of which 45 litres were examined with care, produced 18.

Ingolfiella britannica sp.nov.

With characters typical of the genus (Hansen, 1903; Siewing, 1958); body elongate, much compressed laterally; segments mostly deeper than long (cf. *I. ruffoi* and *I. acherontis* as contrasted with the more elongate *I. abyssi*, *I. petkovskii* and *I. leleupi*). Length of young adults and larger immature 1·4–1·9 mm. (Fig. 1 A).

The front part of the head bears a small but definite lobe, resting in the gap between the two antennae and demarcated from the cephalon proper to which it is attached (Figs. 1 A, 4 A), as Hansen originally describes for *I. abyssi* and *I. littoralis* but not found by other investigators in the species described subsequently.

Each segment of the body carries a single seta on each side of the median line in the anterior half of the segment, the position being near the centre of the segment in the urosome and progressively more anterior in the front part of the mesosome. There is also a seta on the posterior margin in the lower half of the segment. This simple setation appears to be typical of the genus.

The third urosomite appears to be capable of retraction into the second segment so that as much as nearly half of it may be lost to view (in Fig. 1 A it is not quite fully retracted). The rounded telson is similar to that found in other species: on each side it bears one seta and a pair of fine sensory hairs (Fig. 3 J).

Antenna 1 (Fig. 1 B) bears a flagellum of four and an accessory flagellum of three segments. In the accessory flagellum the 2nd segment is twice the length of the others (Fig. 1 D, cf. *I. abyssi*). Aesthetascs are present on the three terminal flagellar segments. In the peduncle segment 1 exceeds the combined length of 2 and 3.

Antenna 2 is typical, with five segments in the flagellum (Fig. 1 C).

The mouthparts (Fig. 1 E) agree closely with Hansen's (1903) description of *I. abyssi*. The *upper lip* and *mandible* appear not to differ; nor does *maxilla* 2, with five setae on its distal lobe and four on the palp (Fig. 1 G). The *maxilla* 1 (Fig. 1 F) is essentially similar: a 2-segmented palp with three or four setae terminally, a distal lobe with six toothed spines (each of an individual shape), and a short proximal lobe which appears to bear only a single seta (as in *I. ruffoi*). The simple *maxillipede* (Fig. 1 H) bears an elongate endite which is apt to lie hidden behind the basal segment of the 5-segmented palp.

All seven peraeon segments have the coxopodites much reduced and scarcely protruding below the body segment; their margin carries at least one seta posteriorly, and usually a smaller one anteriorly. Only segments 3, 4 and 5 bear gills: these are simple oval structures, of about a third the length of the basal segment of the limb (Fig. 3 A–C).

Peraeopods 1 and 2 are modified as gnathopods (Fig. 2), in which, as is characteristic for *Ingolfiella* in contrast with other amphipods, the carpus is enlarged and the functional 'claw' composed of two segments, the propus and dactylus.

In *gnathopod* 1 (Fig. 2 A) the basal segment is, as usual, broad; the carpus is elongate, subtriangular, with the 'palm' continuous with the posterior margin. The point of separation of the palm and posterior margin (opposite the tip of the dactylus) is marked by a small blunt spinous projection (*p*), easily overlooked (cf. *I. abyssi*). Distalwards

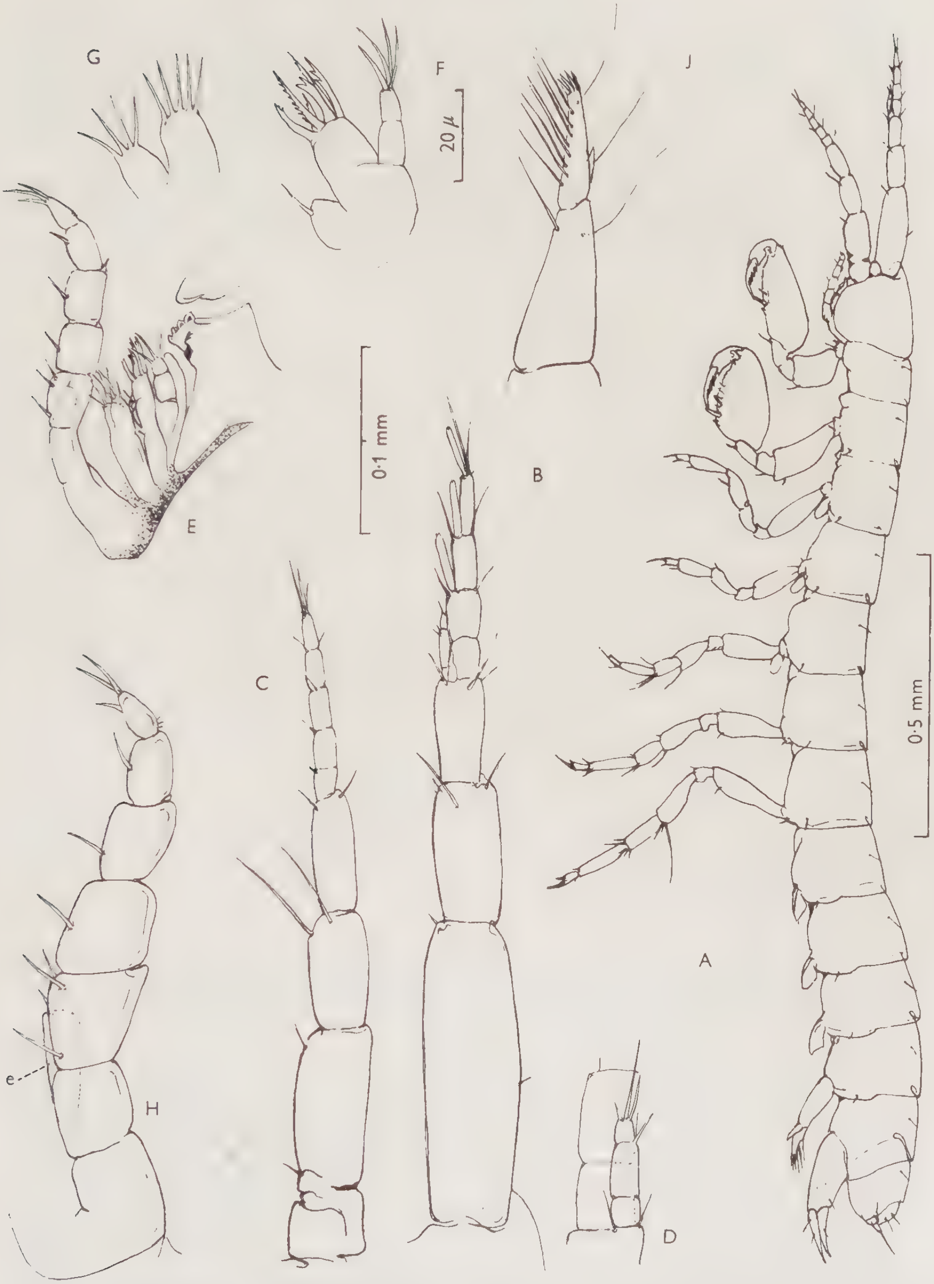

Fig. 1. *I. britannica*. A, Whole animal of 1·71 mm body length (specimen no. 5, chosen as type), probably young male; B, left antenna 1; C, left antenna 2, outer view; D, accessory flagellum of antenna 1 enlarged; E, mouthparts seen from the side; F, maxilla 1, right side, seen from the rear; G, maxilla 2, left side; H, left maxillipede, from rear, *e*, endite; J, right uropod 1 of female seen from inner side, showing long sensory hairs. A, B, C, from specimen 5; D, E, from specimen 11; F, G, H, from specimen 9; J, from specimen 10. The 0·1 mm scale refers only to B, C and J.

of this is a strong linear 'palmar angle' spine, arising on the outer surface, and a little farther on a shorter spine arising on the inner surface. Along the palm a few short setae arise on each margin. The inner side of the propus is straight, but the inner margin of the dactyl is strongly serrate, with four acutely pointed teeth (apart from the elongated tip or 'nail' which might be said to make a fifth tooth). (In *I. abyssi*, *littoralis* and *acherontis* the dactylus of gnathopod 1 is apparently not serrate.)

The carpus of *gnathopod* 2 is broader and possesses a rounded palmar angle which is marked, as in 1, by a short spinous projection (*p*) (this is more strongly developed in *I. abyssi*). Other features are as in gnathopod 1 (see Fig. 2B, C).

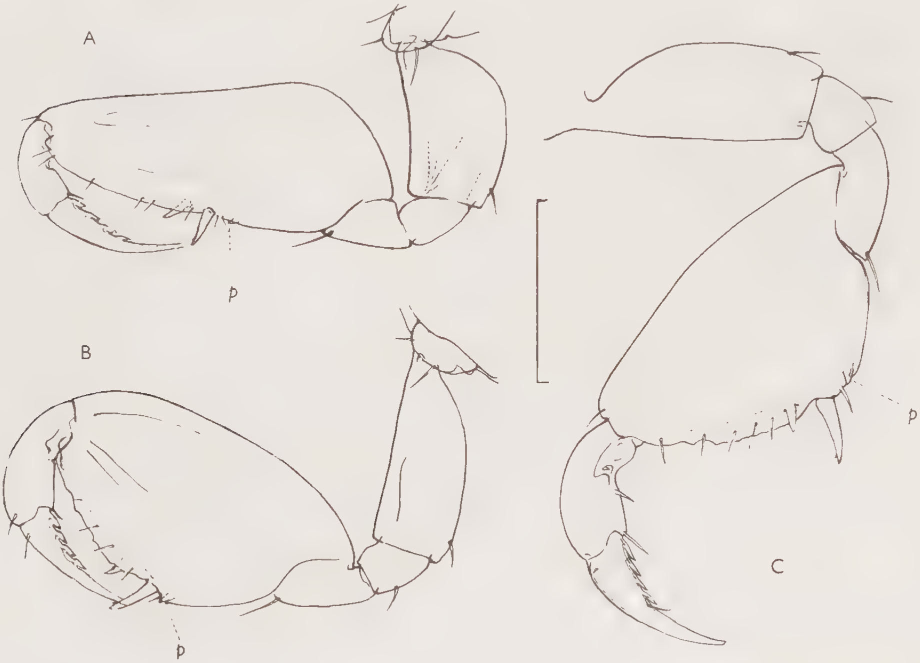

Fig. 2. *I. britannica.* A, Gnathopod 1 of left side, outer view; B, gnathopod 2 of left side, outer view; C, gnathopod 2 of right side, inner view. A and B, from specimen 5; C, from specimen 8. *p*, short spinous projection. The scale represents 0·1 mm.

The remaining five peraeopods (Fig. 3A–E) show progressive changes in shape, 4 and 5 being the shortest, and 7 the longest. As a series these limbs are relatively strong, markedly more so than found in *I. ruffoi* (which, however, they much resemble in shape). The terminal points of the dactyli 5–7 are all long and thin (as in *abyssi*, against *littoralis*). A stout spine arises from the posterior corner of the merus in peraeopods 5 to 7; in 7 it is also elongate, as long as, or longer than, the carpus, and carried in life protruding posteriorly (as shown in Fig. 1). Peraeopod 7 also has a somewhat special armature at the apex of the carpus, where there is a comb of six or seven spines (Fig. 3E): apart from the slender dactylus this limb much resembles that of *I. littoralis*.

The three pairs of *pleopods* (Fig. 4B, C) are broadly triangular and all similar, as in *I. ruffoi* and *I. abyssi*.

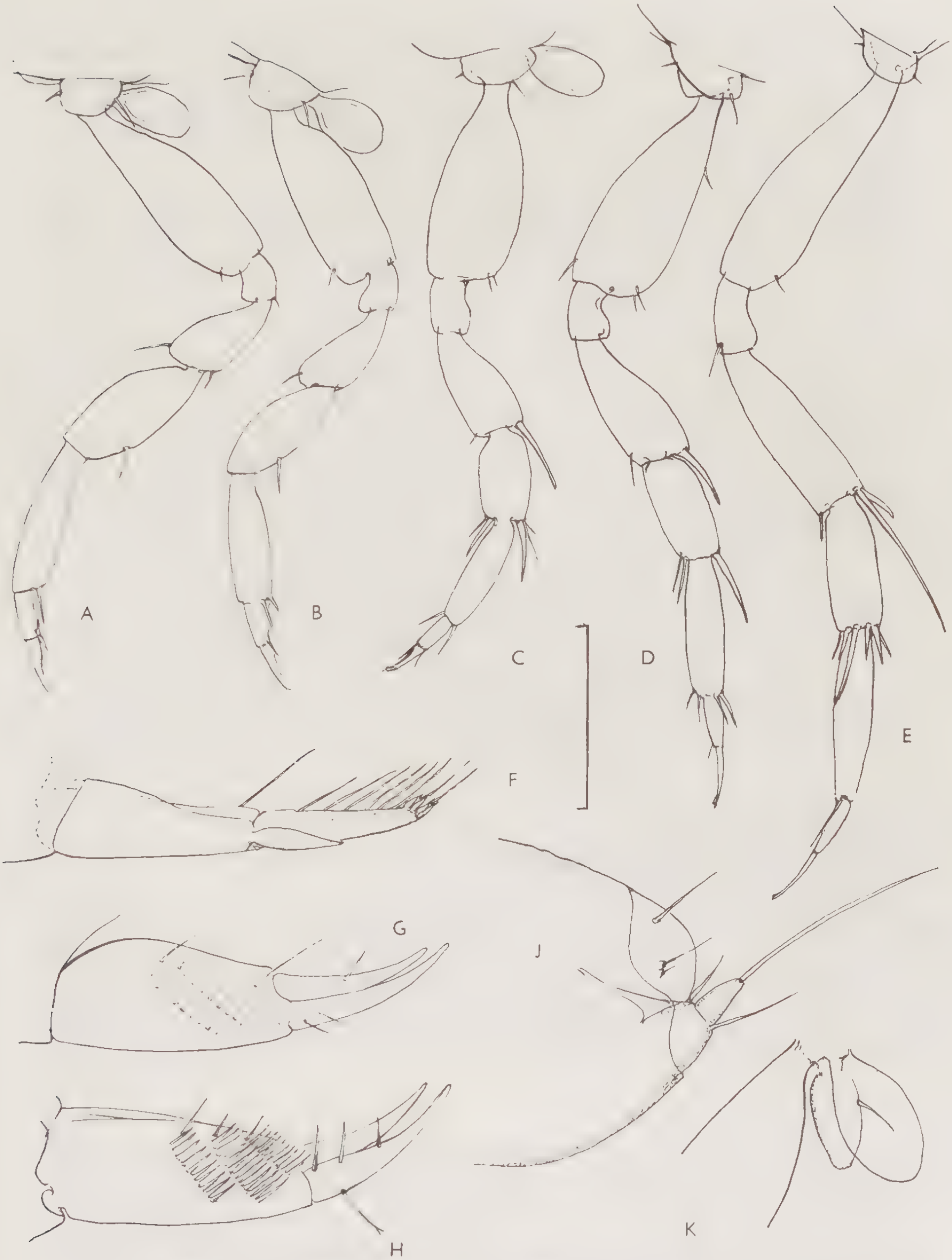

Fig. 3. *I. britannica*. A–E, Peraeopods 3 to 7, left side, outer view; F, G, uropods 1 and 2, left side, outer view (rows of dots represent setal comb showing through); H, uropod 2, right side, inner view; J, telson and uropod 3, seen from left side; K, immature oostegite on base of peraeopod 3. The scale represents 0·1 mm and refers to all but J and K; A–G, from specimen 5; H, from specimen 9; J, from specimen 11; K, from specimen 10.

The uropods are typical of the genus. Uropod 1 (Fig. 3F) has its outer ramus short and unarmed. There are eight long setae and four short terminal spines on the inner ramus. The female, in addition, has three long sensory hairs, one situated near the apex of each segment (Fig. 1J). Uropod 2 (Fig. 3G, H) bears either three or four rows of spines on the inner face of its peduncle. The knob-like uropod 3 bears a long bristle at its apex (Fig. 3J).

Females bear oostegites at the base of peraeopods 3, 4 and 5; these are small oval plates shorter than the accompanying gill, and bear only one short posterior seta when the animal is not breeding (Fig. 3K). (Mature females in breeding condition have not been seen.)

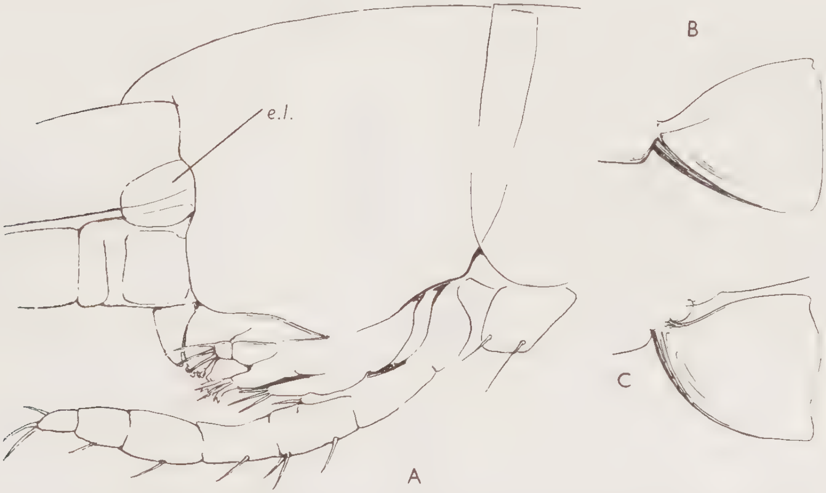

Fig. 4. *I. britannica.* A, Side view of head, mainly to show position of the 'eye-lobe' (*e.l.*) and lie of the mouthparts (specimen 10); B, right pleopod 1, from inside (specimen 11); C, right pleopod 2 from inside (specimen 10).

Type. Mounted specimen (probably young male) of 1·71 mm body length. From dredged Eddystone shell gravel, *c.* 25 fm depth, 9 September 1959. To be deposited in the British Museum. (Position 50° 11·4′ N., 4° 16·6′ W.)

Paratypes. Two (probably young males) from approximately same position as type, 31 March 1959. Sixteen taken at same time as type specimen, some damaged, including two non-breeding females.

Comparison with other species

Ingolfiella britannica is clearly closely related to the Peruvian *I. ruffoi*. From this species it differs positively (i) in its more strongly developed peraeopods, particularly 5–7, and probably also in the stronger spines on the last, (ii) in its somewhat more setose maxillae, and (iii) in its 3-segmented accessory flagellum (2-segmented in *ruffoi*). I cannot be sure that any of the other apparent differences that appear from Siewing's description of *ruffoi* are valid, since small features are easily overlooked. For example the absence, in *ruffoi*, of an 'eye-lobe', a maxillipede endite, and of a small spinous projection delimiting the gnathopod palm, cannot be accepted as certain: all three structures have to be carefully looked for.

From Hansen's original marine species, *I. abyssi* and *I. littoralis*, *I. britannica* differs in having a serrate dactylus on gnathopod 1. *I. abyssi* differs also in its much more attenuate body-form, its more prominent spinose projection at the angle of gnathopod 2, its elongate uropod 1 exopodite, its smaller hind peraeopods, etc. *I. littoralis* has a more oval gnathopod 1, stouter antenna peduncles, and marked differences in certain of the peraeopods.

The two Balkan species show no greater degree of difference although inhabiting fresh water. *I. petkovskii* is at once told from *britannica* by its more shallow body segments and peculiarly modified pleopod 1 (which is linear), but otherwise no very marked divergence is apparent. *I. acherontis* is even closer in its appearance, and, as far as its description goes, only minor differences can be noted, i.e. in lack of more than one tooth on dactylus of gnathopod 1, and in the apparently more pointed shape of its pleopods. It is true that Karaman stated he failed to note an 'eye-lobe' on *acherontis*, and mentions none on *petkovskii*, but this point requires checking.

The remaining species, the larger *I. leleupi* from a cave habitat, shows several special features which distinguish it from the others, and which might justify the erection of a separate genus.

While knowledge of the genus is still so fragmentary, it is much too early to try to assess the degree of relationship between the species known to date. There must be many more awaiting discovery.

Habits

A few of the animals were alive when found, and two at least were fully active at first. They moved by wriggling movements of the body, the compressed form of which seems ideal for progress between gravel particles and in narrow crevices.

A use for the uropod setal combs was shown by one individual which repeatedly tried to clean its gnathopods with them. This behaviour involved bending the body into a loop and pressing the treated limb between the two second uropods.

Habitat

The view may be held that *Ingolfiella britannica*, along with certain other blind colourless forms, is a genuine interstitial animal, and may be expected to be distributed through a depth of the gravel deposit. This is probably not true for most of the many Crustacea to be obtained from the few surface centimetres of the gravel, so that evidence for the above view must be stated.

TABLE 2. NUMBERS OF SMALL MALACOSTRACA PER 45 LITRES OF GRAVEL

9 September 1959

	Agassiz trawl, subsample of 5·7 l. × 45/5·7	Anchor dredge (lower part) full count
(A) A dominant surface species		
Amphipoda		
Leptocheirus pectinatus	34,610	36
(B) Other species numerous at surface		
Amphipoda		
Guernea coalita	726	36
Metopid n.sp.	719	58
Socarnes erythrophthalmus	647	—
Ceradocus semiserratus	632	3
Syrrhoid n.sp.	458	4
Eurystheus lobatus	237	—
Gitana sarsi	205	4
Leptocheirus tricristatus	205	1
Idunella n.sp.	118	3
Megamphopus cornutus	55	4
Maera othonis	47	—
Metaphoxus fultoni	40	1
Liljeborgia kinahani	40	—
Cressa dubia, etc.	16	—
Leucothoë sp., etc.	16	—
Misc. (*Apherusa*, *Nototropis*, *Sympleustes*, *Perierella*, *Normanion*, etc.)	40	3
Isopoda, Tanaidacea, and Cumacea		
Paramunna bilobata	1973	52
Typhlotanais microcheles	324	8
Strongyurella indivisa	205	57
Gnathia oxyurea	189	5
Cumella n.sp.	174	6
Eurycope pygmaea	142	8
Janira maculosa juv.	118	1
Nannastacus spp.	95	5
Paratanais batei	24	1
Microniscid larvae	16	2
Eurydice pulchra, etc.	8	—
Leptognathia sp.	—	1
	7,469	263
(C) Interstitial species distributed through gravel from surface downwards		
Amphipoda		
Bogidiellid n.gen., n.sp.	24	11
Isopoda		
Microcharon harrisi	87	91
	111	102
(D) Interstitial species avoiding the surface		
Amphipoda		
Bogidiella n.sp.	—	10
Ingolfiella britannica	—	18
Tanaidacea		
Strongylura n.sp.	—	7
	0	35
Total per 45 l. of gravel	42,190	436

When the shell gravel has been collected with the Agassiz trawl (now a routine method) which scrapes the surface or at least digs quite shallowly, a density of several hundreds of small Malacostraca is obtained per litre of gravel (evidence from hauls of 15 September 1958, 21 October 1958 and 9 September 1959). Perhaps forty species, of differing abundance, may be got in a haul of 30 l. By contrast, when the more deeply digging Forster 'anchor dredge' is used the equivalent density of Malacostraca is only about 10 per litre of gravel. After an indication of this state of affairs had been got from a haul on 31 March 1959, a careful examination of a large sample (45 l.) taken on 9 September 1959 produced only 436 of these animals. The Agassiz haul, by contrast, collected on the same day, gave a figure of over 42,000 per l. of gravel, as shown in Table 2.

In the 'anchor dredge' sample some species living on or close to the surface are evidently included, but the sample is probably biased towards a depth of between 10 and 20 cm (since it was deliberately taken from the apex of the bag). The composition of this fauna shows a marked preponderance of blind colourless species, and an appreciable proportion of five forms that may be supposed to be genuinely interstitial and surface-avoiding—namely *Microcharon*, two bogidiellids, *Ingolfiella*, and an unknown *Strongylura* with an unusually elongated metasome. Two of these species (group C in Table 2) appear to be equally distributed through the depth of gravel investigated, and the other three, including *Ingolfiella*, seem to avoid the immediate surface of the gravel (group D). None of the group D species have yet occurred in gravel from Agassiz hauls, and for these species at least it can be said that an increase has been found below the surface, albeit the density may remain low even in favourable sites.

DISCUSSION

The recognition of special interstitial forms living in offshore marine deposits raises a further issue. On land, where observation is easier, there is growing evidence of continuity between the faunas of interstitial water, wells, springs, cave pools, underground streams, etc., for the reason that all these habitats are special branches or extensions of the general subterranean water-table through which some species are readily dispersed and others are at least capable of spreading during many generations. There thus arises the notion of a 'hypogean' fauna occupying the not-so-discontinuous medium of subterranean ground-water. May not this be equally true of the terrain below the ocean floor?

Perhaps, indeed, the interstitial fauna of bottom deposits is but the fringe of a more widespread fauna dispersed through rocks below the sea bed, and this supposed 'submarine hypogean' fauna merges with the 'subterrestrial hypogean' of which something is already known. (It may also have broad continuity with the smaller fauna of the dark ocean floor, as does the subterranean fauna with that of deep lake bottoms.) Belief that this indeed may be so is encouraged by the fact that certain malacostracan genera (*Microcharon*, *Bogidiella*) now found to be interstitial in marine deposits are already familiar from continental sites.

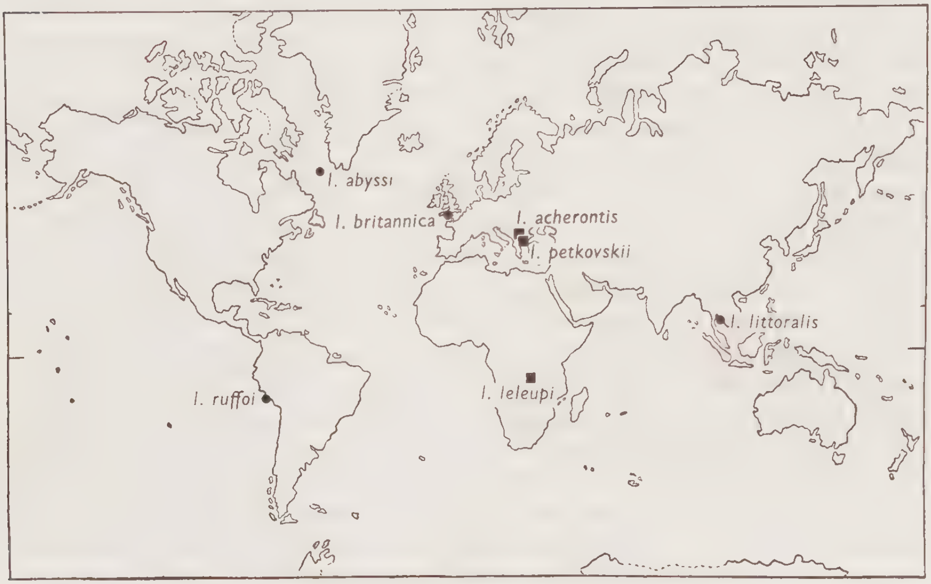

Fig. 5. Distribution of known species of *Ingolfiella* (see Table 1).
●, Marine habitats; ■, freshwater habitats.

The problem presented by what is already known of the distribution of the Ingolfiellidae would now become intelligible. The recorded habitats are just some of the many possible *outposts*, the links between which are not to be found in the seas and surface waters, but in the sub-surface waters that extend beneath both continents and oceans. In this 'hypogean' domain it is supposed that a slow spread and evolution of species has taken place, particularly of a few specialized groups including the ingolfiellids.

On this hypothesis the best chance of finding extensions of range of known species, and the existence of others yet unknown, is to explore hypogean waters. But how to investigate them below the floor of even shallow seas, let alone that at greater depths, presents a formidable oceanographic problem.

SUMMARY

Ingolfiella britannica is described from the Eddystone shell gravel. It is the seventh species of a genus whose distribution has a cosmopolitan aspect, and which occupies an isolated taxonomic position in the Amphipoda.

The species possesses a distinct 'eye-lobe' on the side of the head between the two antennae, as originally described by Hansen for *I. abyssi* and *I. littoralis*, but not seen by subsequent authors in four other species. This is an articulated flap, of very obscure morphological significance.

I. britannica is evidently a true 'interstitial' animal, along with certain other Crustacea occurring with it.

An explanation for the peculiar distribution of *Ingolfiella* is to be sought in the continuity of the 'hypogean' fauna under continents and oceans alike.

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STUDIES ON MARINE ALGAE OF THE BRITISH ISLES: THE GENUS *CERAMIUM*

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(Text-figs. 1–15)

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INTRODUCTION TO THE SERIES

The British Phycological Society was founded in 1952 to serve as a meeting-ground for phycologists, and to carry out a co-ordinated scheme of work on the algae of this country. The specific projects included the production of a *Flora of British Marine Algae* and the publication of a series of biological studies of individual genera and species.

It had been realized for some time that knowledge of the marine algae which occur on the coasts of the British Isles was very inadequate, and recent activities of the Society have made this increasingly obvious. Morphological data are based largely on static anatomical studies and there is little information available on developmental processes. The significance of the range of external form of the thallus in relation to differing conditions of season and environment has not been fully appreciated so that the limits of many genera and species are extremely ill-defined. There is, moreover, a lack of critical nomenclatural studies, with the result that the names currently applied to taxa are largely the result of tradition, whilst knowledge of their ecology and geographical distribution within the British Isles is very incomplete.

It is hoped that the forthcoming publications of the British Phycological Society will help to resolve some of these problems. Work is progressing on the *Flora of British Marine Algae.* The first of the biological studies of individual genera and species is now being published. It is intended that this series of *Studies on Marine Algae of the British Isles* will provide a *concise* but comprehensive survey of taxonomy, nomenclature, morphology, reproduction, life history, ecology and distribution, with particular reference to the British representatives. Such *Studies* will supplement the descriptions, inevitably abbreviated, in the formal taxonomic treatment of the *Flora of British Marine Algae.* It is hoped that these *Studies* will be published at intervals in this *Journal.*

A schedule, giving the essential requirements for *Studies on Marine Algae of the British Isles,* has been published in the *British Phycological Bulletin,* Vol. 1, No. 7, pp. 78–81. Anyone interested, or willing to assist, in the preparation of these *Studies* should communicate with the Secretary of the British Phycological Society, Mr H. T. Powell, Marine Station, Millport, Isle of Cumbrae, Scotland.

ORIGINAL DESCRIPTION

There is much confusion with regard to the generic name *Ceramium,* not only because of orthographic variation, but also because of the diverse species of algae attributed to the genus by the early phycologists. Wiggers (1780) was the first phycologist to use the current spelling, '*Ceramium*', but the names '*Ceramion*' and '*Keramion*' used by Adanson (1763, pp. 13, (8), 535) are now regarded as orthographic variants of this.

The names *Ceramion* and *Keramion* were proposed by Adanson as a substitute for *Ceramianthemum* Donati (1758), now regarded as a synonym of *Gracilaria* Greville (1830). The diverse species attributed to the genus by later authors are as follows:

Wiggers (1780)	*C. filum* (= *Chorda filum* (L.) Stackh.)
	C. fastigiatum (= *Furcellaria fastigiata* (L.) Lamour.)
	C. furcellatum (= *Furcellaria fastigiata* (L.) Lamour.)
	C. confervoides (= *Gracilaria verrucosa* (Huds.) Papenf.)
Gaertner (1788)	*C. plumosum* (= *Ptilota plumosa* (Huds.) Ag.)
Stackhouse (1797)	*C. saccharinum* (= *Laminaria saccharina* (L.) Lamour.)
	C. bulbosum (= *Saccorhiza polyschides* (Lightf.) Batt.)
	C. digitatum (= *Laminaria digitata* (Huds.) Lamour.)
	C. edule (= *Dilsea carnosa* (Schmidel) Kuntze)
	C. palmatum (= *Rhodymenia palmata* (L.) Grev.)
	C. phyllitis (= *Laminaria saccharina* (L.) Lamour.)
	C. esculentum (= *Alaria esculenta* (L.) Grev.)

Roth (1797) referred various species to the genus *Ceramium* and one of these, *C. virgatum* Roth, is a representative of the genus as now delimited. In addition to *C. virgatum,* Roth included in this, his first, treatment of the genus *Ceramium* species now referred to the genera *Chorda, Polysiphonia, Ectocarpus* and *Vaucheria.* Silva (1952) has given a full analysis of the early concepts of *Ceramium* and has argued quite rightly in favour of the conservation of *Ceramium* Roth. The existing grounds for conservation of *Ceramium* against *Apona* Adanson (1763) and *Episperma* Rafinesque (1814) were questionable, in that typification of *Apona* is a matter for conjecture whilst *Episperma*, in the absence of specimens or figures, cannot be typified at all. To clarify this situation, Silva proposed, first, that the problematical *Apona* could be suppressed by appropriate typification and by its acceptance as the nomen rejiciendum of *Lemanea*, and, secondly, that *Ceramium* Roth (1797) should be conserved against *Ceramion* Adanson (1763). These two proposals have now been accepted (see Lanjouw, 1956, p. 206).

TYPE SPECIES

A type species for the genus was not designated by Roth. As *Ceramium* Roth (1797) contains but a single species of the genus as now delimited, Silva (1952) has proposed this species, *C. virgatum* Roth, as the lectotype species:

Ceramium virgatum Roth (1797, p. 148; pl. 8, fig. 1)
  [non *Ceramium virgatum* Hooker & Harvey (1848, p. 445)]
= *Ceramium rubrum* (Huds.) Agardh (1811, p. 17), fide C. Agardh, loc. cit.

The earlier proposal by Schmitz (1889) of *Ceramium rubrum* as the type species, repeated by Kylin (1956), is incorrect in that *Conferva rubra* Hudson (1762), its basionym, is not listed as such by Roth in his original treatment of the genus.

Roth's herbarium was transferred from Oldenburg to the Botanisches Museum, Berlin, in 1930, and there destroyed by bombing in March 1945 (Pilger, 1953). A few Roth specimens are still in existence in other herbaria, but attempts to locate duplicate material of *C. virgatum* have proved unsuccessful. The figure of *C. virgatum* given by Roth (1797, pl. 8, fig. 1) is not good, but it is sufficiently clear to permit identification; in the absence of a specimen this figure should be designated as the type of *C. virgatum* Roth.

SYNONYMY

Dictiderma Bonnemaison (1822, p. 185)
Hormoceras Kützing (1841,[1] p. 730)
Gongroceras Kützing (1841,[1] p. 730)
Echinoceras Kützing (1841,[1] p. 731)
Acanthoceras Kützing (1841,[1] p. 731)
Chaetoceras Kützing (1847, p. 34)
  nec *Chaetoceros* Ehrenberg (1844, p. 198)
  nec *Chaetoceras* Kützing (1849, p. 138)
Trichoceras Kützing (1849, p. 680)
Celeceras Kützing (1849, p. 683)
Pteroceras Kützing (1849, p. 690)
Ceramothamnion Richards (1901, p. 257)

As Silva (1952) has commented, Bonnemaison (1822) was the first author to distinguish clearly between the species now attributed to the genera *Ceramium* and *Polysiphonia*, placing species of the former in his *Dictiderma*, for which *Conferva rubra* Huds. [= *Ceramium rubrum* (Huds.) Ag.] was designated as the type species. In his revision of the genus *Ceramium*, Kützing (1841, 1847, 1849), in a series of proposals, suggested that the genus should be divided into nine smaller genera, viz. *Hormoceras*, *Gongroceras*, *Echinoceras*, *Acanthoceras*, *Chaetoceras*, *Trichoceras*, *Celeceras*, *Pteroceras* and *Centroceras*. Of these, only the last, *Centroceras*, has been retained by subsequent authors and this would appear to be well founded. The other proposals made by Kützing were not accepted generally at the time, possibly because of the constant changes of generic circumscription in the various publications and possibly because of the large number of very ill-defined species described by Kützing for these genera. By modern taxonomic standards there is no justification for the generic subdivision proposed by Kützing, other than the separation of *Centroceras*. The genus *Ceramothamnion*, proposed by Richards (1901) for his new species *C. codii*, does not differ from *Ceramium* in any essential feature. Mazoyer (1938) refers *Ceramothamnion codii* to the genus *Ceramium*, rightly stating that there is no justification for the creation of a distinct genus for this species. This opinion has been repeated by this and other authors (Feldmann-Mazoyer, 1940, in Børgesen, 1952; Dixon, 1958), but it should be noted that *Ceramothamnion* was still retained by both Fritsch (1945) and Kylin (1956).

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[1] Kützing's paper '*Ueber* Ceramium *Ag.*' is published in the last part of volume 15 of the journal *Linnaea*, which is dated 1841. Howe (1914, p. 155) has indicated, quite correctly, that Kützing (1849), in *Species Algarum*, consistently cites '1842' as the date of publication of this paper. Because of this, Howe has regarded 1842 as the true date of publication. Setchell & Gardner (1924), on the other hand, have pointed out that in the earlier '*Phycologia Generalis*' (Kützing, 1843), '1841' is cited, equally consistently. Attempts to determine the precise date of publication have not been successful, so that at the present time it would seem best to retain the date of 1841 for this publication until further information is available.

In addition to the synonyms cited above, Børgesen (1953) has recently proposed the new genus *Ceramiella*, for *Ceramium huysmansii* Weber v. Bosse (1923) and has suggested that the *C. maryae* of the same author might also be referable to this genus. Mme Feldmann has commented (in Børgesen, 1953) that in her opinion there is no justification for the creation of a distinct genus for *C. huysmansii* and that this species should be referred to *Centroceras*. At the present time, the morphological information on *Ceramiella huysmansii* is so inadequate that no decision as to the correct taxonomic position of this species can be made. Under the circumstances, Dawson (1954) has adopted the most logical attitude, by retaining both *C. huysmansii* and *C. maryae* in *Ceramium*, pending further study.

DESCRIPTION OF GENUS

Genus of marine and brackish waters.

Thallus of uniaxial construction, erect or prostrate, 0·1–30·0 cm in length, red, brown or purple in colour; axes filiform, 0·1–1·5 mm in diameter, pseudo-dichotomously or irregularly branched, differentiated into axial cells and cortex; axial cells large (up to 1·5 mm in length), ovoid or cylindrical, hyaline or faintly pigmented; cortex formed by the aggregation of the filaments of limited growth, arranged in bands encircling the axial cells and forming a partial or complete investment.

Tetrasporangia borne laterally on filaments of limited growth, partially or completely embedded, tetrahedral or cruciate.

Sexual thalli dioecious, rarely monoecious; spermatangia hyaline, developing superficially from the ultimate cells of the lateral branches of limited growth, forming colourless patches of variable size on the surface of the cortex; carpogonial branches and auxiliary cells developing from the basal cells of the filaments of limited growth near to the apex of an axis; carposporophyte exserted, naked, sessile, subtended by a number of adventitious axes.

MORPHOLOGY AND DEVELOPMENT OF THE THALLUS

The thalli of all Florideae are built up by the aggregation of filaments, which result from the division of apical cells. Some of these filaments are of unlimited growth and form the axes of the thallus; the majority, however, are of limited growth and these form the cortical investment to the axes of unlimited growth. In *Ceramium*, the axes each contain a single filament of unlimited growth, that is, they are uniaxial in construction.

Apical segmentation

The basic pattern of segmentation was first outlined by Cramer (1857). Since that date there have been numerous descriptions of apical structure and segmentation.

Each segment formed by the transverse division of the principal apical cell of an axis of unlimited growth divides further to produce from four to nine pericentral cells. The mother-cells remaining after the formation of pericentral cells do not divide again but increase in size to form the axial cells (Fig. 1).

The pericentral cells are formed in a definite sequence, with a fixed orientation. The first pericentral cell formed is cut off on the outer face of each segment; the 'outer face' being determined by the previous pseudodichotomy (Fig. 2F). The remaining pericentral cells are cut off successively in pairs to form a ring of cells at the apical pole of each segment (Figs. 1, 2A–E). This orientation of the pericentral cells is of very great importance in that it is associated with the orientation of many other structures, such as spines, tetrasporangia, etc.

The axial cells

The axial cells are formed from the mother-cells remaining after the formation of the pericentral cells. The enlargement of the axial cells is of considerable significance in that it has a profound effect upon the longitudinal growth of the axes. A comparison of the length and volume of newly formed and mature axial cells in various species of *Ceramium* (Table 1) gives a good indication of the degree of enlargement. The enlargement of the axial cells is not related directly to the age of the cell, but shows considerable variation in different parts of the plant. This phenomenon is discussed in greater detail later, with particular reference to its taxonomic implications.

TABLE 1

	Size when formed (μ)	Size when mature (μ)	Increase in length	Increase in volume
C. rubrum	4 × 16 × 16	380 × 316 × 300	95 ×	35,000 ×
C. echionotum	4 × 20 × 20	420 × 240 × 220	105 ×	14,000 ×
C. shuttleworthianum	4 × 12 × 12	220 × 70 × 80	55 ×	2,000 ×

Note. The dimensions, length, depth and breadth, are mean values based on measurements of 400 cells.

The increase in size of the axial cell is associated with the development of a large vacuole. In maturing axial cells there is a peripheral layer of

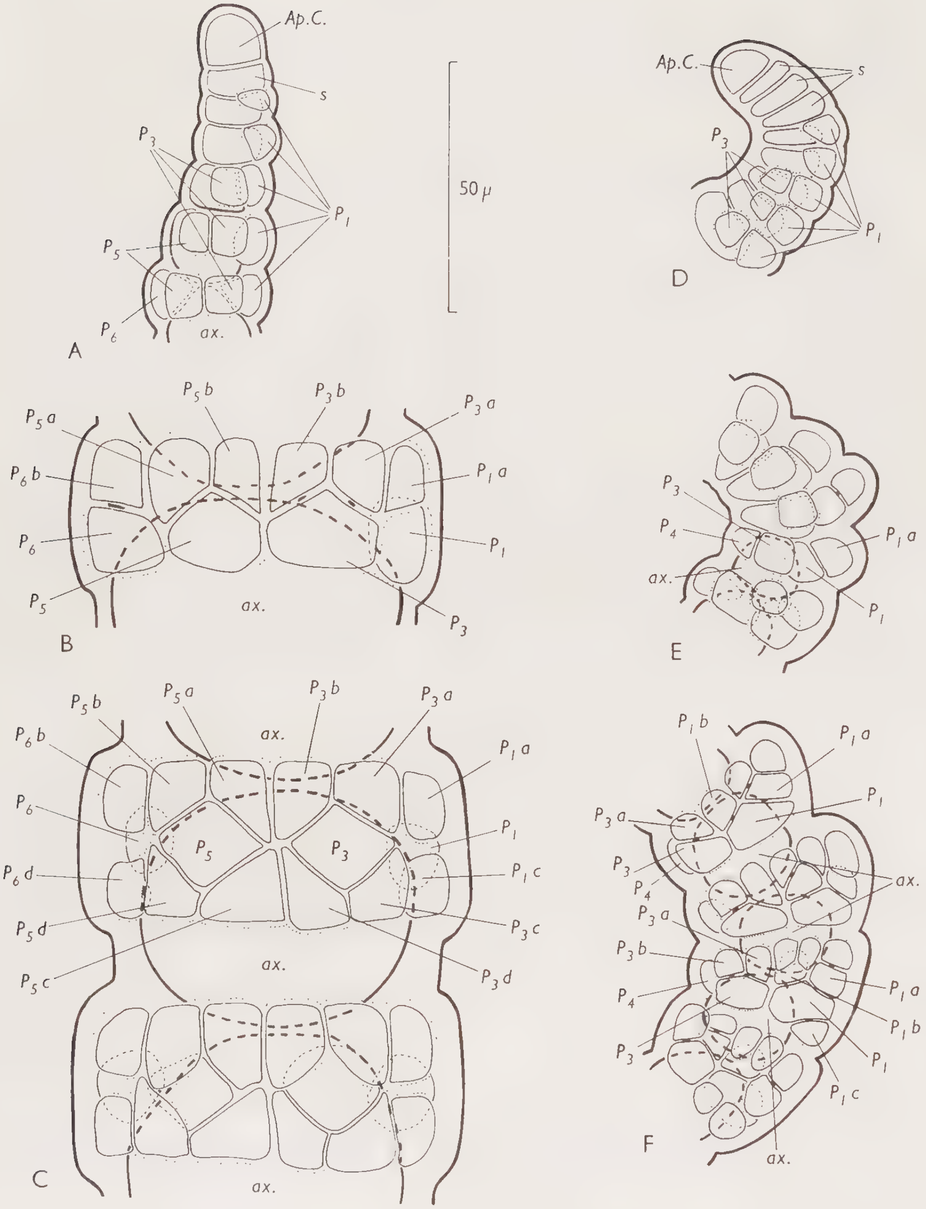
Ap.C.
s
P3
P1
P5
P6
ax.
A
50 μ
Ap.C.
s
P3
P1
D
P5 b
P3 b
P3 a
P5 a
P6 b
P1 a
P6
P1
P5
ax.
P3
B
P3
P4
P1 a
ax.
P1
E
P5 b
P5 a
P3 b
P3 a
P6 b
ax.
P1 a
P6
P5
P3
P1
P6 d
P1 c
P5 d
P3 c
P5 c
ax.
P3 d
C
ax.
P1 b
P1 a
P1
P3 a
P3
P4
P3 a
P3 b
P4
P3
ax.
P1 a
P1 b
P1
P1 c
F
ax.

Fig. 1. Apical segmentation and the development of the cortical band in the genus *Ceramium*. The basic pattern of segmentation in straight (A–C) and curved (D–F) apices is fundamentally identical, although there are obvious differences associated with the degree of curvature. *Ap.C.*, Apical cell of an axis; *s.*, segment produced by the transverse division of the apical cell of an axis; *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_1a, P_1b, acropetally directed apical cells of lateral branches of limited growth, produced from P_1; P_1c, P_1d, basipetally directed apical cells of lateral branches of limited growth, produced from P_1.

cytoplasm lining the wall of the cell and a central strand connecting the pit-connexions in the apical and basal walls. Elongate convolute chromatophores are distributed in the peripheral layer of cytoplasm. In those species where the cortex forms a complete investment to the axial cells, the chromatophores, even in the young cells, are only slightly pigmented. As the cells age, the pigmentation disappears completely. The chromatophores are more conspicuous in those species where the axial cell is exposed because of the incomplete cortical investment, but even so degeneration occurs with age.

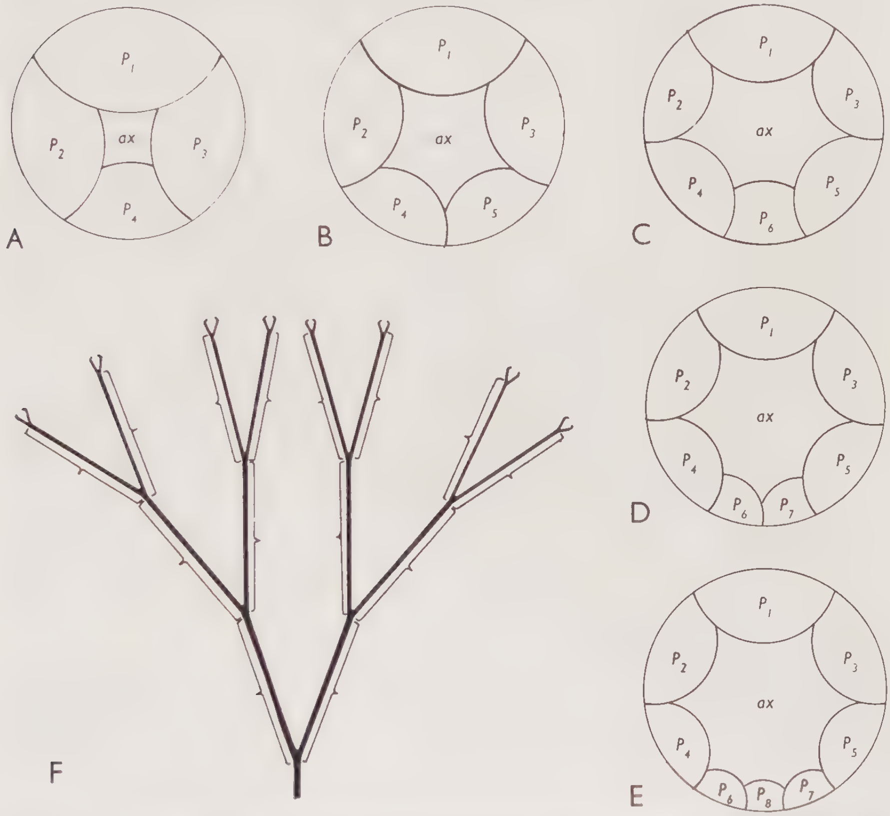

Fig. 2. A–E, Sequence of divisions in segments from which 4, 5, 6, 7 and 8 pericentral cells are formed; F, outwardly directed orientation of the first pericentral cells, in relation to the pseudo-dichotomy of the axes; the positions of the first pericentral cells in each 'sector' are indicated by brackets. *ax.*, Axial cell; P_1, P_2, P_3, etc., pericentral cells, numbered in order of formation.

The presence of a central strand of cytoplasmic material in the axial cells of *Ceramium* has been discussed or figured by various authors (Moore, 1885; Petersen, 1908; Schiller, 1913; Phillips, 1926; Dammann, 1930, 1932; Celan, 1939*a*, *b*; Feldmann-Mazoyer, 1940; Feldmann & Feldmann, 1946; Funk, 1955). Phillips (1926, p. 277) has rightly commented that Moore (1886) mis-interpreted the observations of Hick (1884) on *C. acanthonotum* (= *C. shuttleworthianum*). Hick's observations, which are somewhat obscure, do not refer to the central cytoplasmic strand. These strands, the 'trabeculae' of Phillips, are readily discernible in fresh material, even in completely-corticate axes, but, as Phillips has commented, their preservation in dried herbarium specimens is very variable. The cytoplasmic strands are solid, cylindrical structures when first formed and they may contain large numbers of crystalline granules. The single nucleus is situated in the centre of the strand in the newly formed axial cell, but, as the cell matures and enlarges, the nucleus migrates to the basal end of the strand, where it eventually disintegrates. In the majority of axial cells, the central cytoplasmic strands eventually appear to break down completely, although in some specimens they are quite distinct even in axes which have persisted from one season to the next and which must be at least 1 year old.

Both Phillips (1926) and Feldmann-Mazoyer (1940) have described the penetration of intracellular filaments into the axial cells of *Ceramium*. Similar penetration of the axial cell has been described by Drew (1945) in the genus *Batrachospermum*. The intracellular filaments, which obviously must be regarded as modified lateral branches of limited growth, arise in the cortex and pass into the axial cells. A study of the early stages of penetration confirmed Phillips's observation that the penetration into the axial cell takes place through the pit-connexion between the axial cell and a pericentral cell, but it was not possible to determine the precise position in the cortex from which the filaments had originated. In a single example, it appeared that an intracellular filament had penetrated the basal pit-connexion of an axial cell and passed into the axial cell below. The factors controlling the development of intracellular filaments are unknown. The occurrence of these filaments is relatively rare in the British Isles, but in the three examined specimens in which this phenomenon occurred the majority of axial cells contained intracellular filaments.

Formation of the lateral branches of limited growth

Each of the pericentral cells gives rise to four apical cells, two of which are directed acropetally and two basipetally (Fig. 1). One or more further apical cells may be formed in those species where the cortical band is well developed. The apical cells thus formed segment to produce the much-branched lateral branches of limited growth.

The lateral branches of limited growth derived from a single segment of the principal apical cell of an axis aggregate to form an encircling band of cortex, which is adpressed to the axial cell from which it has arisen. Each cortical band envelops the lower part of the axial cell above, in addition to

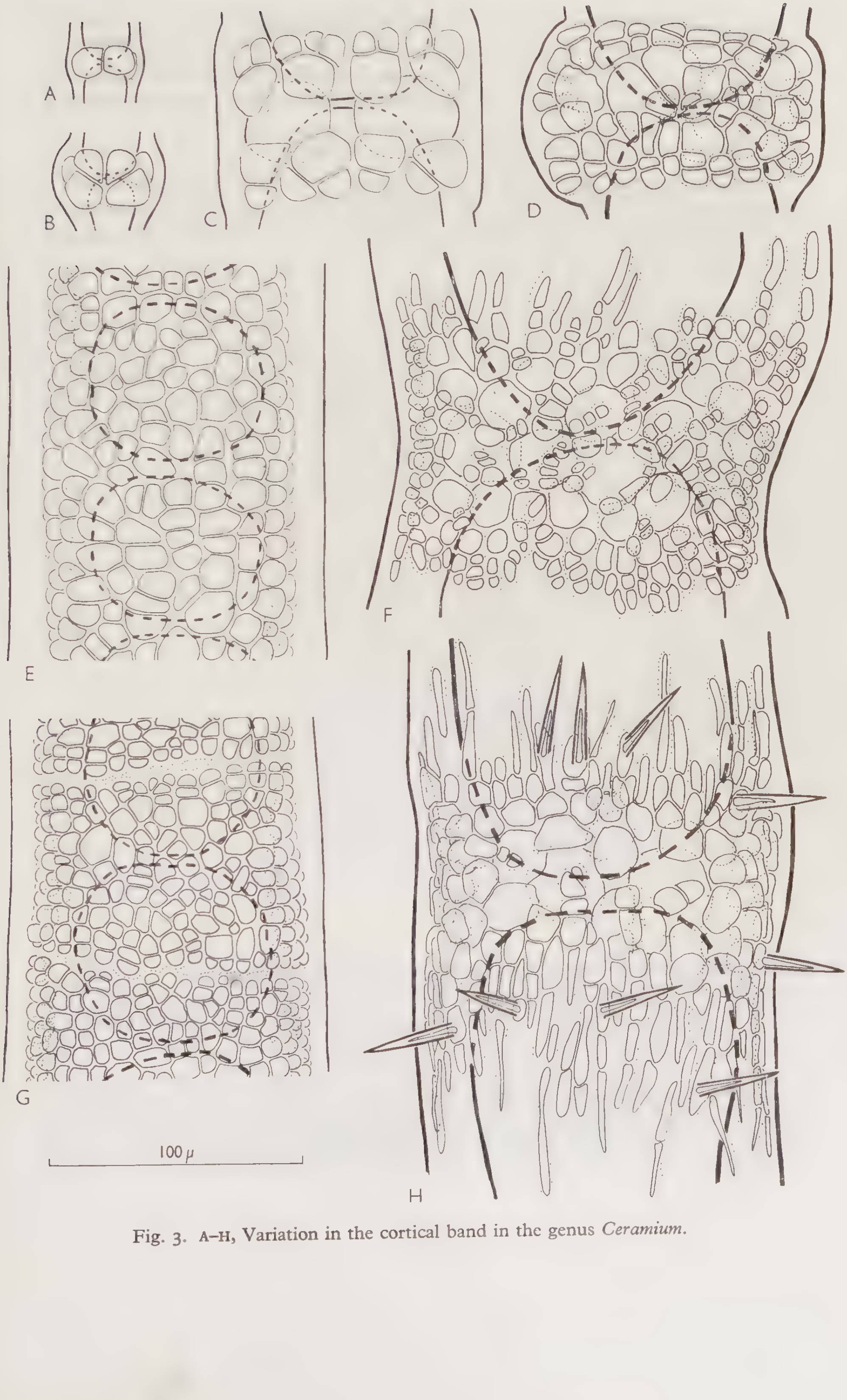
A
B
C
D
E
F
G
H
100 μ

Fig. 3. A–H, Variation in the cortical band in the genus *Ceramium*.

the upper part of the parent axial cell. Adjacent cortical bands may remain distinct, so that the cortex forms only a partial investment to the axial filament, or they may merge, so that the cortex forms a complete investment to the axial filament (Fig. 3 E). The degree of cortication is of some taxonomic significance.

Formation of the lateral branches of unlimited growth

The axes of all species of *Ceramium* are profusely branched. Lateral branches of unlimited growth are formed either in the very characteristic pseudo-dichotomous manner in the apical region, or adventitiously in mature parts of the thallus (Fig. 4).

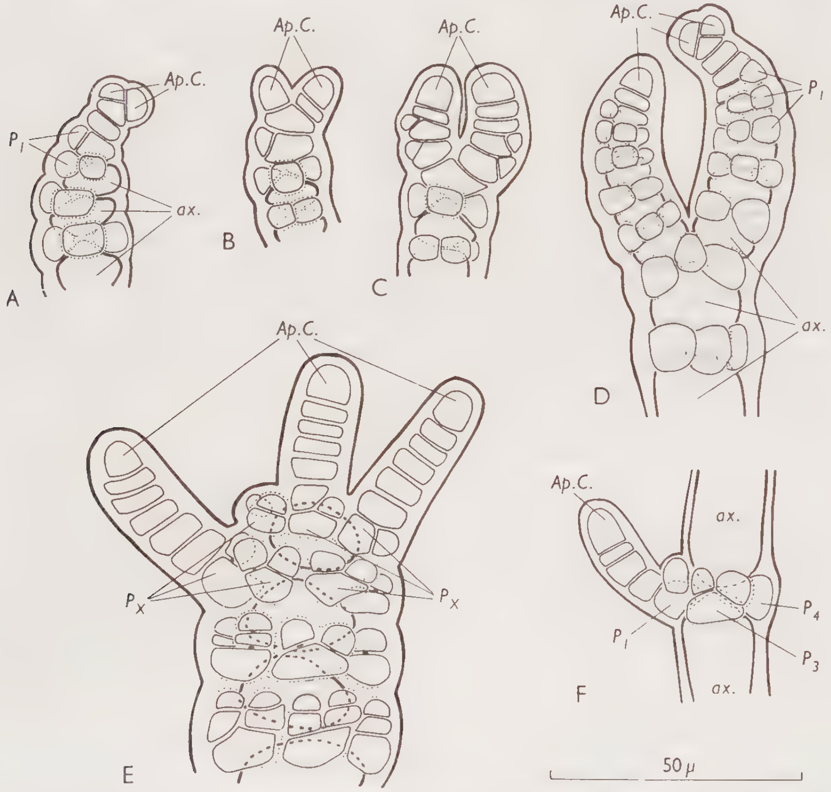

Fig. 4. Origin of lateral branches of unlimited growth. A–D, Pseudo-dichotomy of the apex; E, origin of adventitious lateral branches of unlimited growth in a damaged axis; F, origin of adventitious lateral branches of unlimited growth in an undamaged axis. *Ap.C.*, Apical cell of an axis; *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_X, pericentral cell of unknown status.

The pseudo-dichotomous branching of the apical region of the thallus is initiated by the appearance in the thimble-shaped apical cell of two inclined walls, which cut off the two new apical cells. The first apical cell is cut off eccentrically on the inner face relative to the previous 'dichotomy', whilst the second apical cell is cut off on the outer face, opposite to the first (Fig. 4A, D). As a result of this orientation, the axes of the thallus tend to lie in a single plane, although secondary distortion may disturb the initial arrangement. The two new apical cells segment transversely a number of times before they undergo a further pseudo-dichotomy (Fig. 4A–D). If the growth of the pairs of derivative apical cells is balanced throughout the thallus, then the thallus has a characteristic flabellate appearance, but frequently there are differences in rate of growth between the apical cells of each pair so that the thallus is somewhat racemose.

Adventitious lateral branches of unlimited growth occur frequently in all species of the genus *Ceramium*. They may develop prolifically in apparently normal specimens, although they occur frequently in specimens which have been grazed by animals or damaged in some other way, and in specimens in which tetrasporangia or carposporophytes have developed.

The apical cell of an adventitious lateral branch of unlimited growth is formed by the transformation of the apical cell of a lateral branch of limited growth (Fig. 4E, F). In old, fully developed specimens, after extensive damage, adventitious lateral branches of unlimited growth may arise from any part of the thallus.

The germination of tetraspores *in situ* has been observed on a few occasions, in various species of *Ceramium* (see p. 349), although the phenomenon is not of frequent occurrence, not having been reported by previous investigators. The germlings produced by this 'internal' germination of tetraspores grow out from the parent axis and in this way give rise to a form of 'false branching'. In some examples, the attachment of the germling to the parent is firm and the tissues of the two organisms blend together almost imperceptibly so that it is very difficult to distinguish between an adventitious lateral branch of unlimited growth and the product of 'internal' germination of a tetraspore. In other cases, particularly in those species where the cortical bands form an incomplete investment to the axial filament, the germination of tetraspores *in situ* is very obvious and the attachment is usually very weak so that the germlings are easily detached.

Hairs

Unicellular hairs, similar to those which have been described in numerous species of the Florideae (Berthold, 1882; Möbius, 1892; Rosenvinge, 1911; Feldmann-Mazoyer, 1940) occur frequently in the genus *Ceramium* (Fig. 5A–D). The hairs occur in all parts of the thallus, but normally they are most abundant in the apical regions. A hair may develop from any superficial cell of the thallus. A small uninucleate primordium, with dense granular contents, is cut off from the superficial cell (Fig. 5B, C), which then functions as a basal cell. Rapid elongation takes place, so that when mature the hairs measure up to 100 μ in length. During the process of elongation, the nucleus degenerates and a large vacuole is formed so that the cytoplasm forms a small, meniscus-like mass at the apex of the mature hair. The hairs are thin-walled and very fragile, so that they are easily damaged. Unlike the spines, the hairs cannot withstand desiccation, so that most are destroyed in the preparation of dried herbarium specimens.

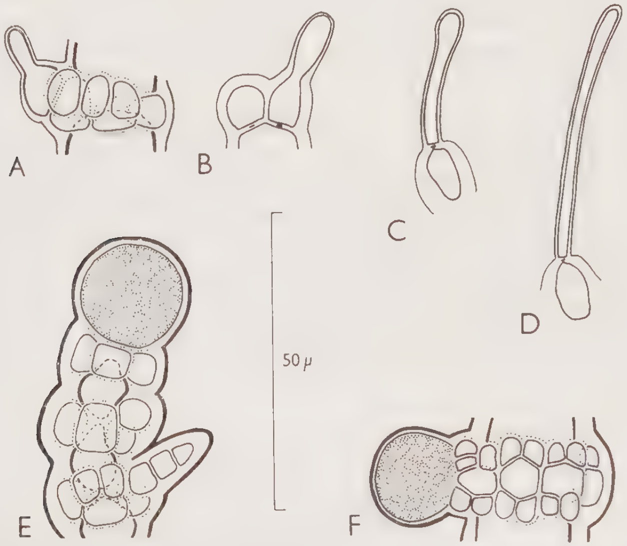

Fig. 5. A–D, Stages in the development of a hair; E, occurrence of *Eurychasmidium tumefaciens* in the apical cell of an axis; F, *E. tumefaciens* in a cell of the cortical band.

Setchell & Gardner (1924, p. 777), in the original description of *C. fimbriatum*, comment on the 'single row of thick, short, unseptate hairs, which are soon deciduous, on the outer curves of the apices'. As figured by these authors (pl. 26, figs. 43, 44), these hairs are much shorter and stouter than the hairs which occur in other species of the genus. Dawson (1954, fig. 55*a*) also gives a figure of this species but it is somewhat crude and little information as to the nature of the hairs can be obtained from it.

Glandular cells

Glandular or vesicular cells ('cellules secretrices', 'Blasenzellen') are widespread in the Ceramiaceae (Kylin, 1915, 1927; Ollivier, 1927, 1928; Feldmann-Mazoyer, 1940). In *Ceramium*, where they were first reported by Reinbold (1906, p. 576), they are formed by the transformation of superficial cortical cells, particularly in the apical regions of the thallus. During development, the cortical cell enlarges slightly, the nucleus and chromatophores degenerate. When mature the contents of the glandular cell are colourless and translucent.

Degeneration takes place very rapidly so that glandular cells tend to be found principally in the apical portions of the axes.

Rhizoids

The thallus is attached to the substrate by unicellular and multicellular rhizoids (Fig. 6). In some species these are formed only at the base of the thallus, but in species of prostrate habit adventitious rhizoids develop from all parts of the plant.

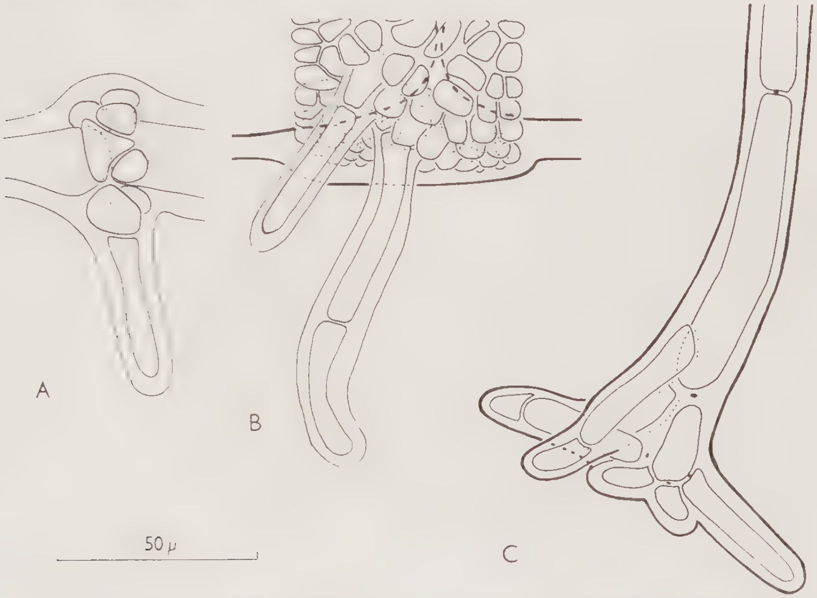

Fig. 6. A–C, Origin and structure of the rhizoids in the genus *Ceramium*.

The rhizoids are formed by the modification of superficial cortical cells. The primordium may remain undivided to form a unicellular rhizoid or it may divide once or twice (Fig. 6 B) so that a multicellular rhizoid is formed. Occasionally a number of divisions occur at the apex of a rhizoid giving rise to a multicellular attachment organ (Fig. 6 C). Unicellular rhizoids occur more frequently than the multicellular type, but both may be formed from adjacent cortical cells.

The primary basal rhizoid formed in the early stages of development of spore-germlings (see p. 349) frequently penetrates the substrate to which it is attached (Fig. 9 D, E), but in most instances the adventitious rhizoids form only a superficial attachment to the substrate. There are some previous reports of the penetration of the substrate by adventitious rhizoids (Feldmann-Mazoyer, 1940), but during the present investigation this has been observed only very infrequently.

Spines

Spine-like structures occur in a number of species of *Ceramium*, of which four occur in the British Isles. In the four British species, spines develop in the meristematic apical regions of the axes, although occasionally they may be formed as adventitious structures in mature fully developed thalli. In order to differentiate between the two types of spine, the former will be referred to as 'primary spines'.

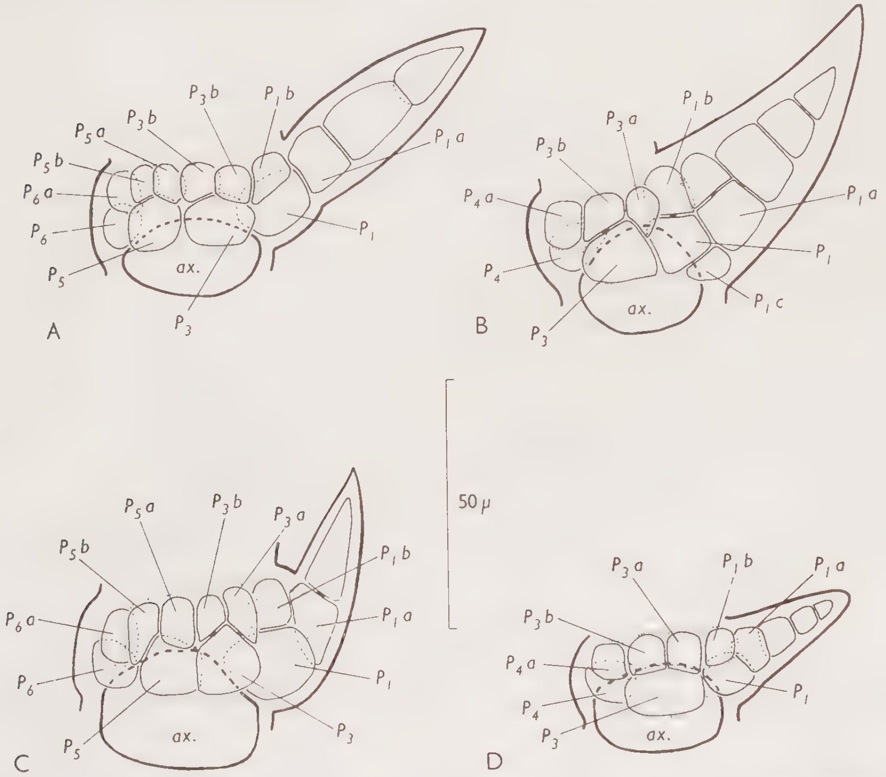

Fig. 7. A–D, The comparative morphology of the spines in the four British spine-bearing species of *Ceramium*. A, *C. ciliatum*; B, *C. shuttleworthianum*; C, *C. echionotum*; D, *C. flabelligerum*. *ax.*, Axial cell; P_1, P_2, P_3, etc., pericentral cells, numbered in order of formation; P_1a, P_1b, acropetally directed apical cells of lateral branches of limited growth, produced from P_1; P_2a, P_2b, acropetally directed apical cells of lateral branches of limited growth, produced from P_2; P_1c, basipetally directed apical cell of lateral branch of limited growth.

A primary spine is formed by the modification of one of the two acropetal primordia of lateral branches of limited growth which develop from each pericentral cell. The degree of modification varies from species to species. In all cases, some cells at the base of the lateral branch are incorporated into the cortical band, whilst the terminal cell or cells project to form the spine.

In *C. echionotum* the spine consists only of the terminal cell of the lateral branch of limited growth, whereas in *C. ciliatum*, *C. shuttleworthianum* and *C. flabelligerum*, the spine is formed from a number of cells (Fig. 7A–D). Primordia of lateral branches of limited growth which are to form spines are formed before, and grow very much more quickly than adjacent primordia. Because of this, a spine may be fully developed before the second acropetal primordium of a lateral branch of limited growth is cut off from the parent pericentral cell. The frequency of formation of spines varies considerably in the four species, but, if any spines are formed in a segment, then the first-formed will always occur on the outer face of the axis relative to the previous pseudodichotomy. If more than one primary spine is formed, these will tend to develop from acropetal primordia of adjacent pericentral cells. The conversion into spines of both the acropetal primordia of a given pericentral cell is of very rare occurrence and has been observed only twice by the present author.

Adventitious spines may develop in profusion from any part of the thallus, but they occur usually in the older, more mature parts. In structure the adventitious spines resemble the primary spines, but they are formed by the modification only of the ultimate part of a lateral branch of limited growth. Unlike the primary spines, the orientation of the adventitious spines is not determined and their arrangement is therefore very irregular (Fig. 3H).

Feldmann-Mazoyer (1940, p. 153) has differentiated between the spines found in *C. echionotum* and those of the other species of *Ceramium*, claiming that the spines of *C. echionotum* are modified hairs, whilst those of other species are modified lateral branches of limited growth. The development of the spine in *C. echionotum* will be discussed in detail in a later publication, but it would appear that the incorrect interpretation of the spine structure in *C. echionotum* by Feldmann-Mazoyer results from the failure to study in detail the development of the spine in relation to the development of the cortical band. The spines of *C. echionotum*, like those of *C. ciliatum*, *C. flabelligerum* and *C. shuttleworthianum*, are modified lateral branches of limited growth (Fig. 7A–D).

The occurrence of spines has been reported in a number of other species of *Ceramium*, including: *C. horridum* Setchell & Gardner (1924, p. 777), *C. sinicola* Setchell & Gardner (1924, p. 773), *C. paniculatum* Okamura (1896, p. 36), *C. hamatispinum* Dawson (1950, p. 122), *C. puberulum* Sonder (1845, p. 52), *C. monacanthum* J. Agardh (1894, p. 29), *C. uncinatum* Harvey (1855, p. 257). The spines of *C. monacanthum* are formed by the modification of lateral branches of limited growth, but in other species the information available is so scanty that it is not possible to comment on the origin of the spines. In one or two of the species it would appear from the published figures that the term 'spine' is being used to describe short axes of unlimited growth rather than lateral branches of limited growth; further, detailed investigations of the morphology of the 'spine' in these species are obviously required.

Galls

Superficial gall-like outgrowths, or warts, are of frequent occurrence in the genus *Ceramium*. Chemin (1932) has given an account of the galls found in *C. rubrum*, but apparently he failed to appreciate either the frequency of occurrence of these structures or the taxonomic implications of his observations. Galls have been observed in almost all the British species of the genus during recent investigations (Dixon, unpublished).

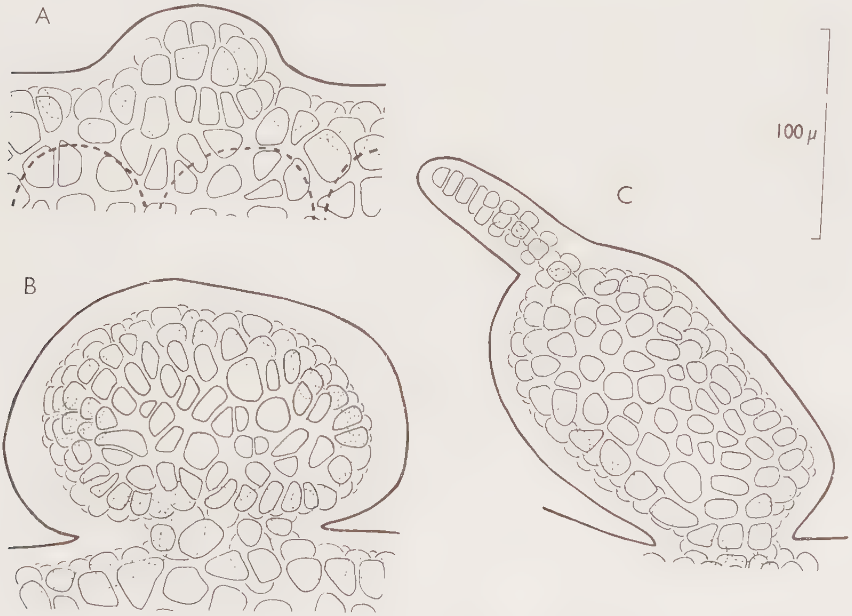

Fig. 8. A, Early stage of development of a gall; B, later stage of development; C, axis differentiating from the tissues of a gall.

Galls occur with varying frequency; some specimens of *Ceramium* may show only a single example, whilst others may be covered with them. All stages of development may occur and it is obvious from a study of their development that these structures are nothing more than proliferations of the outermost cells of the cortex. During the early stages of development (Fig. 8A) the galls are hemispherical, with a smooth surface, but with age the surface becomes corrugated and in the oldest specimens the proliferations are irregularly lobed. The cells at the periphery of the gall are similar in appearance and size to those of the outermost layers of the cortex, whilst the internal cells are large and often hyaline. In those species of *Ceramium* in which spines are formed, spines may develop also from the surface of the proliferation. This phenomenon appears to have been overlooked by previous investigators, although Kützing (1862, pl. 95*b*, *d*) does give figures of what appear to be galls covered with spines, in *C. monile* (= *C. puberulum*). Hairs, similar to those which develop on the cortical bands, are of frequent occurrence. In one specimen the proliferations were giving rise to structures which resembled normal rhizoids and in another to an axis of unlimited growth (Fig. 8C). The galls are deeply pigmented, red or brown in colour. The largest measure up to 1 mm in diameter and are clearly visible to the naked eye.

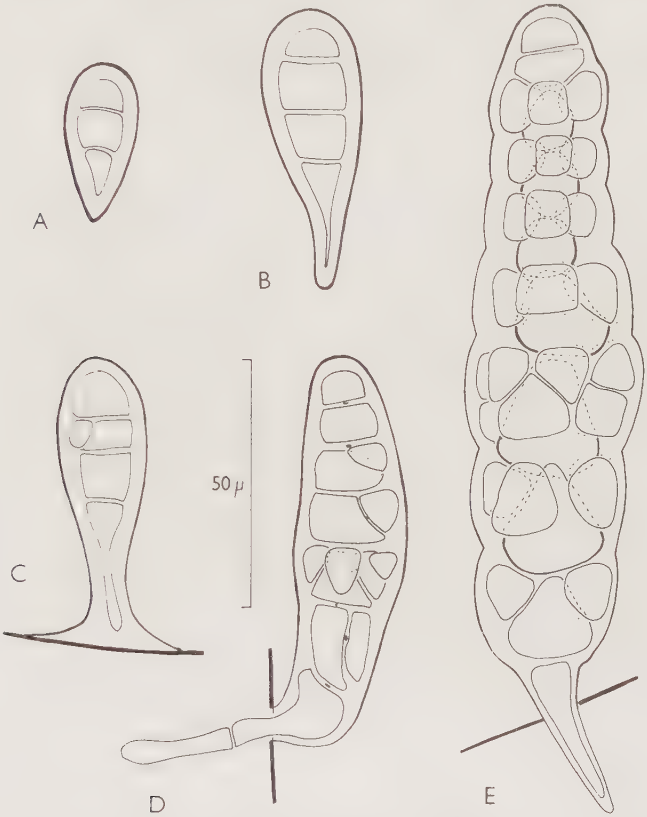

Fig. 9. A–E, Stages in spore germination.

Cantacuzene (1930), as a result of a long investigation of the galls of *Saccorhiza polyschides* and *Chondrus crispus*, has shown that a bacterium occurs in the proliferations of these two species and that similar structures may be produced by inoculation of a culture of this bacterium. Chemin (1932) was unable to offer any explanation for the origin of the proliferations of *C. rubrum*.

It has not been possible to determine the reasons for the development of galls during recent investigations (Dixon, unpublished). No evidence of external damage could be detected even in the youngest examples, neither could the presence of bacteria be detected in fresh or preserved material.

Galls have been mis-interpreted by several investigators, who have regarded them either as carposporophytes or as parasporangia or polysporangia. The taxonomic implications of these mis-interpretations will be discussed in a subsequent paper.

Life-span of the thallus

The thalli of the species of *Ceramium* may be either annual or perennial. Environmental conditions and the substrate to which it is attached appear to be the principal factors determining the life-span of the thallus.

Although the thallus may be relatively ephemeral, developing from a spore, becoming fertile and then decaying completely in the autumn, the thallus may persist for at least two years. The survival of large fragments is relatively rare, other than in pools and under sublittoral conditions, but in the intertidal region, minute fragments of the basal portions of thalli have been shown to persist through the winter on such diverse substrata as rotting wood, concrete, Manx slate and in debris under populations of *Mytilus*. These minute fragments regenerate in the spring to give rise to new erect fronds. It is unfortunate that although the development of new erect axes from these minute fragments which have persisted through the winter can be observed frequently, no information as to whether the process can be repeated indefinitely was obtained, although this would appear to be very probable.

Such information on survival and perennation is obviously of vital importance in any discussion of life histories and the alternation of phases in species of the genus.

Spore germination

The germination of tetraspores and carpospores has been described for various species of *Ceramium* (Derick, 1899; Tobler, 1903; Killian, 1914; Kylin, 1917; Chemin, 1937). All germlings, derived from either carpospores or tetraspores, are of the bipolar type characteristic of the Ceramiaceae. The differences between carpospore and tetraspore germination are insignificant. Little or nothing is known of the germination of the so-called 'polyspores' or 'paraspores'; the only information available is the figure given by Schiller (1913) which is indistinguishable from a similar stage of germination of a carpospore or tetraspore.

In most cases the spore attaches itself to the substrate by a cushion of mucilage and divides to form a principal apical cell and a rhizoid rudiment. The apical cell segments rapidly to form an axis whilst the rhizoid rudiment elongates to form the down-growing basal rhizoid. The rhizoid usually penetrates the mucilage cushion and it frequently grows into the substrate if this is of suitable texture (Fig. 9D, E). The segments produced by the division of the principal apical cell give rise to axial cells and cortical bands in the usual way. Frequently the first-formed cortical bands are slightly aberrent in that development of the band is somewhat restricted, although the pattern of segmentation is normal . In spine-bearing species, the spines may be malformed or even absent in the lowermost segments. The first pseudodichotomy occurs after 12 or even 18 segments have been produced, even in species where only 6 or 7 segments are normally formed between successive 'dichotomies'. At this stage of development, adventitious rhizoids develop from the lowermost cortical bands aiding the attachment to the substrate.

Although not reported by previous investigators, the germination *in situ* of both carpospores and tetraspores has been noted. Previously, it would appear that germination of carpospores *in situ* has been reported only in genera where the carposporangia are enclosed in a compact sterile envelope, i.e. *Bonnemaisonia* (Drew, 1949), *Lemanea* (Mullahy, 1952). In *Ceramium*, where the carposporangia are exposed and the carpospores more easily liberated, such germination *in situ* is surprising, but in a number of examples, the preliminary elongation of the carpospores has been noted and even the formation of the first division wall.

The germination of tetraspores *in situ* occurs more frequently. The mode of division is identical with that of liberated spores, the germlings produced growing epiphytically on the parent axis to produce a type of 'false branching'. The occurrence of such 'false branching' may or may not be very obvious and the rigidity of the attachment of the germling to the parent varies considerably. The occurrence of 'false branching' resulting from the internal germination of tetraspores is easily detected in incompletely corticate thalli, because of the very obvious disturbance of the cell arrangement in the cortical bands. Furthermore, in incompletely corticate thalli the attachment is extremely weak, so that the majority of the germlings are easily detached. In completely corticate thalli, germlings resulting from the germination of tetraspores *in situ* are frequently attached very firmly so that they resemble normal adventitious axes. Occasionally, because of the disturbance of the pattern of segmentation of the parent axis, their origin is obvious, but in most cases detailed microscopic examination is necessary before the product of germination of a tetraspore *in situ* can be distinguished from an adventitious lateral branch of unlimited growth.

In *Ceramium*, the proliferations produced by the internal germination of a tetraspore appear to develop each from a single spore and, without exception, all the examples studied were sterile. Osterhout (1896) has given an account of the *in situ* germination of tetraspores in *Rhabdonia* (= *Agardhiella*) *tenera*, but in this species the germlings are formed, apparently, by the aggregation of the segmentation products of all the four spores of the original tetrasporangium. Furthermore, Osterhout has reported the occurrence on the proliferations in *Rhabdonia* of spermatangia and 'cystocarps' as well as tetrasporangia, in addition to the occurrence of all three types of reproductive structure on the one proliferation; it is obvious that a more detailed examination of *Rhabdonia* is necessary.

The frequency of occurrence of internal tetraspore germination in *Ceramium* varies considerably. A few examples were noted from time to time, but occasionally a plant would be collected in which the majority of tetrasporangia had germinated internally. It is not possible to offer any explanation for this phenomenon.

The germination of tetraspores *in situ* is of considerable importance in any discussion of the occurrence of tetrasporangia and sexual organs on the same thallus. Although Osterhout (1896) commented that 'proliferations resembling those of *Rhabdonia* occur on tetrasporic plants of *Cystoclonium*, *Gracilaria* and other higher Florideae', subsequent investigators appear to have ignored or overlooked the possibility of internal germination of tetraspores in these and other genera of the Florideae.

STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS AND CARPOSPOROPHYTE

Sexual and tetrasporic plants, which are morphologically identical, have been described for most species of *Ceramium.* According to Kniep (1928), most species are dioecious, although Rosenvinge (1924) has reported the occurrence of spermatangia on carpogonial plants of *C. fruticulosum* and a single monoecious plant of *C. pedicillatum* was detected in material collected by Dr J. A. Kitching at Lough Ine, Ireland. The life history is interpreted generally as a regular sequence of sexual, carposporic and tetrasporic phases, but there is little direct evidence to support this assumption (Petersen, 1928; Westbrook, 1935). As in other genera of the Ceramiaceae (Kniep, 1928; Drew, 1944), there have been reports of the occurrence of sexual organs and tetrasporangia on the same thallus, as follows:

C. ciliatum, tetrasporangia and carposporophytes (Woronichin, 1909)
C. circinatum, spermatangia and tetrasporangia (De Toni, 1922)
C. pedicillatum, tetrasporangia and sexual organs (Davis,1910)
C. rubrum, tetrasporangia and sexual organs (Davis, 1905).

It should be noted that in a number of species tetrasporic plants have a much wider distribution, extending further to the north, than the sexual plants. Accessory methods of reproduction ('polysporangia' and 'parasporangia') occur in a number of species, whilst Chemin (1928) and other authors have described vegetative propagation.

Tetrasporangia

The tetrasporangia of *Ceramium* are produced in the cortical bands, developing laterally from cells of the lateral branches of limited growth. The number of tetrasporangia formed in a given cortical band varies considerably. In those cortical bands where a single tetrasporangium develops, it is formed always in the second position, that is, on the outer face of the axis relative to the previous 'dichotomy'. In most species, however, a number of tetrasporangia are produced in each cortical band, distributed in a whorl, or, where the number is excessively large, irregularly arranged (Fig. 10).

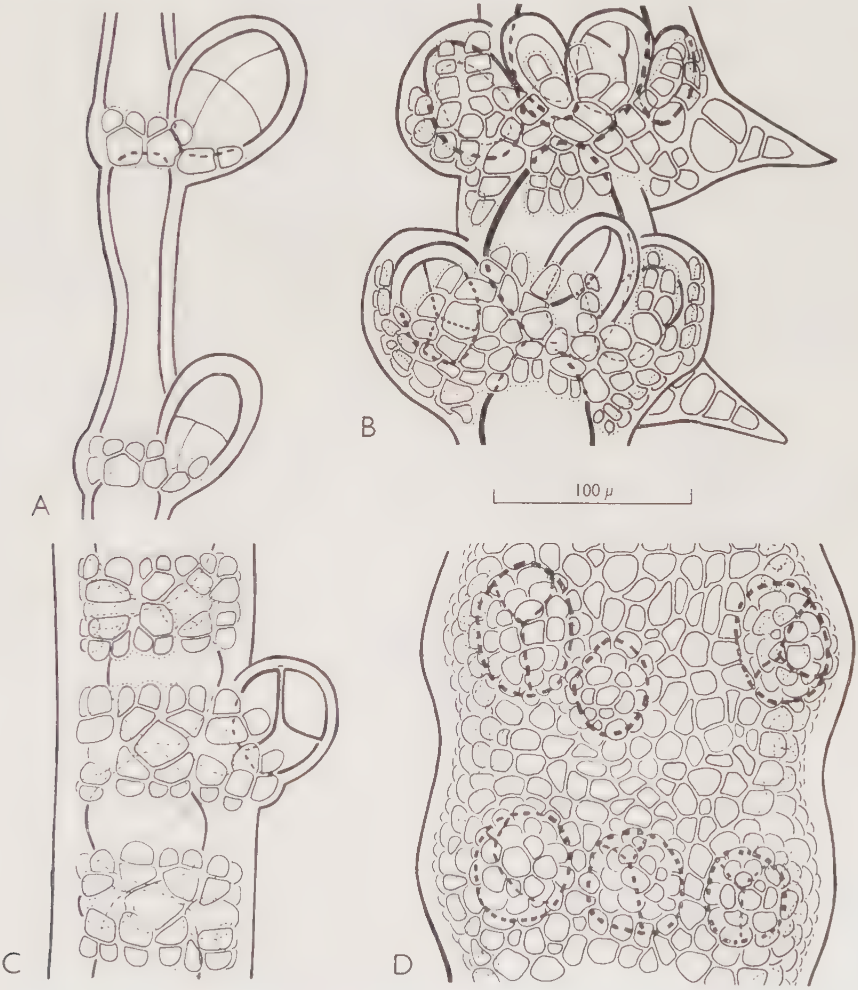

Fig. 10. A–D, Arrangement of tetrasporangia in the genus *Ceramium*.

The primordia of tetrasporangia are relatively small, but when mature the tetrasporangia measure 30–110 × 20–60 μ. The division is usually tetrahedral, although a cruciate arrangement of tetraspores has been reported in a number of species (cf. Rosenvinge, 1924, p. 373). In the British Isles, the cruciate arrangement occurs frequently in certain species (Fig. 10A).

The degree of emergence of the mature tetrasporangium from the cortical band is determined by the size of the sporangium and the extent of development of the band (Fig. 10A–D). In those species with continuous cortication, the tetrasporangia tend to be immersed completely (Fig. 10D), whilst in those species with interrupted cortication, they are partially emergent. Where the development of the cortical band is extremely restricted, as in *C. codii*, the tetrasporangia appear to be produced externally from it (Fig. 10A).

Spermatangia

The spermatangia of *Ceramium* have been studied repeatedly (Buffham, 1884, 1888; Petersen, 1908; Grubb, 1925; Feldmann-Mazoyer, 1940).

The spermatangia are formed superficially from mother-cells derived from the apical cells of the lateral branches of limited growth. In those species where the cortex is well developed, the apical cells are transformed directly into spermatangial mother-cells, but in *C. codii* (see Feldmann-Mazoyer, 1940, fig. 59*b*), and in other species where the cortical band is poorly developed, the apical cells of the lateral branches of limited growth divide once or twice before giving rise to spermatangial mother-cells. Each spermatangial mother-cell forms from three to five spermatangia, each of which produces a single spermatium.

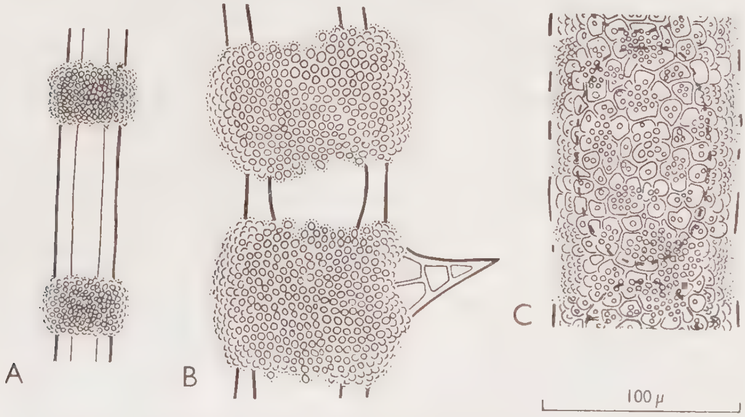

Fig. 11. A–C, Arrangement of spermatangia in the genus *Ceramium*.

The spermatia are colourless and the pale patches formed by the aggregation of spermatangia are very characteristic. Where the cortical bands are distinct, the entire surface of each band is covered with spermatangia, but where the cortical bands are confluent, the spermatia tend to form patches of irregular outline (Fig. 11).

The carpogonial branch and the development of the carposporophyte

Although the carpogonial branch and carposporophyte of *Ceramium* have been investigated repeatedly (Janczewski, 1876; Phillips, 1897; Kylin, 1923; Rosenvinge, 1924; Miranda, 1929*a*, *b*; Dammann, 1930) the details of their development given by the different authors are somewhat contradictory. Many of the accounts are fragmentary and it may be that the confusion results from the inadequate examination of a number of different species. A full investigation of the structure and development of the carpogonial branch and carposporophyte throughout the genus *Ceramium* is urgently required.

In all investigated species of *Ceramium*, a pericentral cell functions as the supporting cell of the carpogonial branch. As far as can be ascertained, the supporting cell is always derived from the first-formed pericentral cell of a segment, so that the carpogonial branch develops in the second position, that is on the outer face of the axis relative to the previous 'dichotomy'. In sexual thalli, the carpogonial branches are produced intermittently. Frequently, the first-formed pericentral cells from a number of adjacent segments in an axis are converted into supporting cells; such fertile regions occur at intervals along the axes separated by sterile regions. The number of supporting cells produced in depauperate specimens is reduced considerably, so that carpogonial branches occur only at infrequent intervals.

As in all Ceramiaceae, the carpogonial branch is four-celled. The carpogonium is relatively small, but the trichogyne reaches a length of up to 50 μ. The cells of the carpogonial branch are smaller than the adjacent cells of the cortical band. The conversion of the first-formed pericentral cell into the supporting cell and the formation of one or more carpogonial branches disrupts the regular pattern of development of the cortical band. A supporting cell is larger than the normal first-formed pericentral cell from which it is derived and only one or two of the four lateral branches of limited growth normally formed from a pericentral cell are produced by a supporting cell. As a result of the disturbance of the pattern of segmentation, the position of a carpogonial branch can be detected relatively easily. It should be noted that the hairs, which may bear a superficial resemblance to trichogynes, are merely added to the normal vegetative structure, with no disturbance at all.

According to Kylin (1923, p. 63) a single carpogonial branch is formed from each supporting cell in *C. rubrum*, although in material of this species from the Channel Islands (Dixon, unpublished), the formation of two carpogonial branches from the same supporting cell was observed in a number of specimens. Janczewski, Phillips and Rosenvinge have reported the occasional formation of two carpogonial branches in other species of the genus.

A detailed study has been made of the development of the carpogonial branch in a species of the *C. diaphanum/strictum* complex (sensu Feldmann-Mazoyer, 1940), collected near Prah Sands, Cornwall. In this material, the formation of two carpogonial branches from a supporting cell occurred frequently (Fig. 12B), but such supporting cells were intermixed with others from which only a single carpogonial branch had developed (Fig. 12C, D). No explanation can be offered to account for this phenomenon.

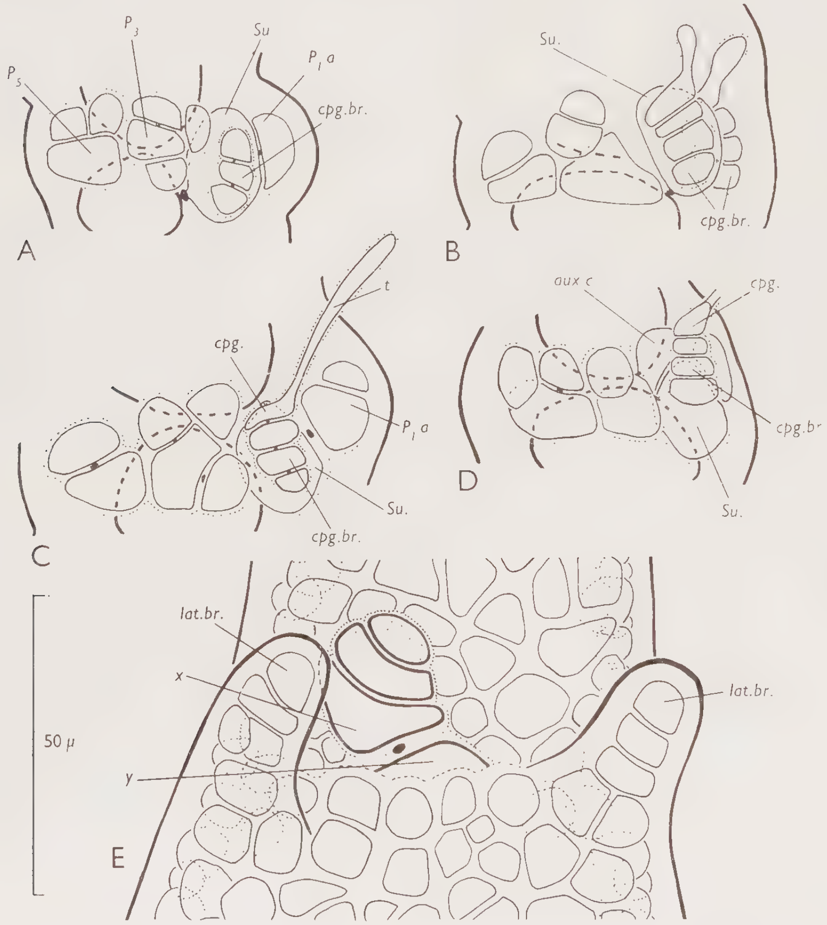

Fig. 12. A, B, Development of the carpogonial branch; C, mature carpogonial branch; D, early post-fertilization stage; E, initial stage in the development of the carposporophyte. *aux.c.*, Auxiliary cell; *cpg.*, carpogonium; *cpg.br.*, carpogonial branch; *lat.br.*, adventitious lateral branch of unlimited growth; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_1a, acropetally directed apical cell of lateral branch of limited growth, produced from P_1; *Su.*, supporting cell, formed by the modification of the first-formed pericentral cell; *t.*, trichogyne; *x.*, *y.*, cells at the base of the carposporophyte, whose origin cannot be stated with certainty.

As in all Ceramiaceae, the auxiliary cell is cut off from the supporting cell subsequent to fertilization (Fig. 12D).

Details of the development of the carposporophyte are a little confused. Various authors have given a few observations on stages of development in certain species, but the absence of an over-all survey of carposporophyte development throughout the genus is a serious deficiency. Taking into account both personal observations and the descriptions of previous authors, it is possible to summarize the information available in a general way. It is thought that communication is established between the carpogonium and the auxiliary cell, and that subsequently one or more primordia are formed from the auxiliary cell. There are differences of opinion (cf. Kylin, 1923; Miranda, 1929*b*) as to whether the auxiliary cell divides into two cells before the formation of primordia. The further development of the carposporophyte results from the segmentation of these primordia. Fusions between certain cells have been reported by most previous investigators, but it must be stated that there is some evidence from personal observations to indicate that the fusions are not obligatory and that the cells involved are not always determined specifically. It is obvious that careful and detailed investigations are necessary for the solution of these problems.

The young carposporophyte forms a cluster of cells on the surface of the thallus (Fig. 12E). Because of the orientation of the carpogonial branches, the carposporophyte frequently lies on the outer side of the axis relative to the previous 'dichotomy'. The carposporophyte is situated usually in a small depression in the side of the axis (Figs. 12E, 13A, B), resulting from the diminished enlargement of the adjacent axial cells and the absence of some of the lateral branches of limited growth from the pericentral cell which developed into the supporting cell. As the carposporophyte enlarges, adventitious lateral branches of unlimited growth are formed from filaments of limited growth of the segment below it. The number of adventitious axes thus formed is often very characteristic, for instance in *C. shuttleworthianum* a single adventitious axis is produced, whilst in other species up to five or even seven such axes may be formed. The growth of these axes is restricted so that they rarely exceed 2 mm in length. When fully mature, the carposporophyte is encircled by these axes which form a loose, incomplete involucre.

Accessory methods of reproduction

Sporangia containing more than four spores, to which the terms 'polysporangium' and 'parasporangium' have been applied, have been reported in several species of *Ceramium*. Throughout the Florideae, the application of these terms is extremely confused. Schiller (1913) attempted to differentiate between the two types of sporangium, but in *Ceramium*, the system suggested by him proved to be inapplicable (cf. Rosenvinge, 1924, p. 399). Drew (1937, 1939), as a result of detailed cytological and morphological studies of selected examples of sporangia, has suggested that in the Florideae the sporangia containing more than four spores are of two categories, (*a*) those which are *not* homologous with tetrasporangia and which are purely accessory, e.g. the 'parasporangia' of *Plumaria elegans* (Drew, 1939), (*b*) those which *are* homologous with tetrasporangia, e.g. the 'polysporangia' of *Spermothamnion snyderae* (Drew, 1937) and other Florideae (Westbrook, 1930), but the lack of data has prevented the general acceptance of this scheme and the terms 'polysporangium' and 'parasporangium' are still applied indiscriminately by different authors to the same structure. In the genus *Ceramium* the position is complicated by certain authors failing to recognize gall-like proliferations which have been misidentified and described as 'parasporangia' or 'polysporangia'. In the following account a number of descriptions have had to be discounted because of the possibility of such confusion in the absence of an illustration (e.g. Kylin, 1907).

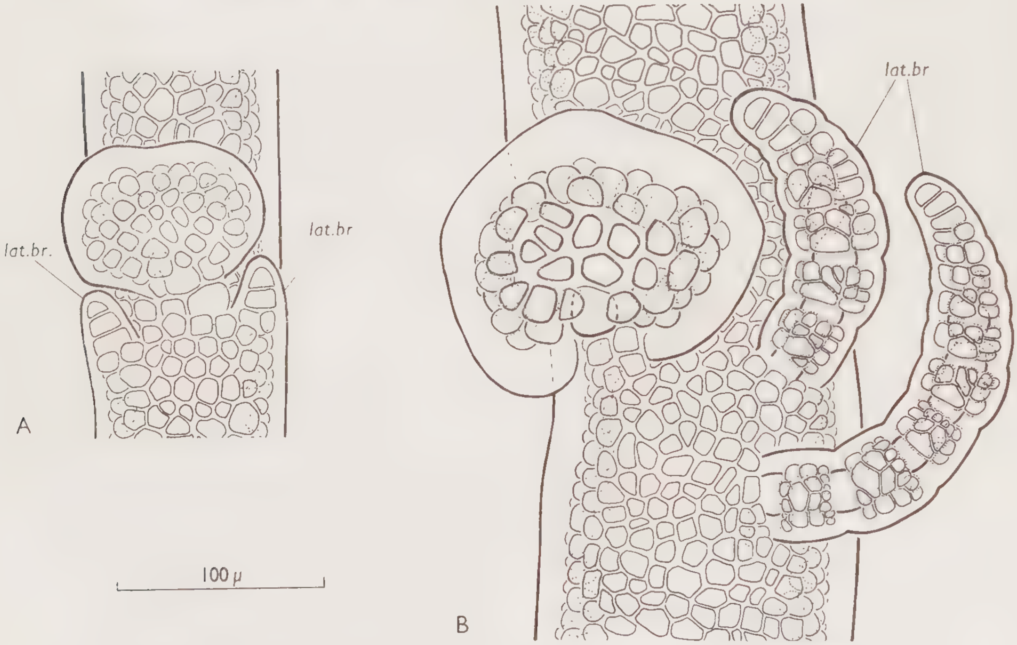

Fig. 13. A, B, Later stages in the development of the carposporophyte. *lat.br.*, adventitous lateral branch of unlimited growth.

There are two types of accessory reproductive structure in species of the genus *Ceramium*. These differ in structure, position and development.

Lateral sporangia, which contain from five to twelve spores, and which bear a close resemblance to tetrasporangia, have been figured in a number of species, including *C. diaphanum* (Petersen, 1908, figs. II and IV), *C. strictum*

(Lakowitz, 1929, fig. 491), '*C. deslongchampsii*' (Rosenvinge, 1924, fig. 321) and *C. vertebrale* (Rosenvinge, 1924, fig. 325). There are no reports of the occurrence of these sporangia in the British Isles, and despite a widespread search during the past seven years, no indication of their occurrence could be found. Although little is known about the development of these lateral sporangia, from the figure given by Rosenvinge (1924, fig. 313) it would appear very probable that these sporangia should be interpreted as modified tetrasporangia and the term 'polysporangia' applied to them. A detailed cytological study of their development is urgently required. It should be noted that there is one difference between the lateral sporangia and tetrasporangia in that tetrasporangia are embedded in the cortical band, whilst the lateral sporangia are formed superficially. No information is available on the mode of germination of the 'polyspores' or of their significance in relation to the life-histories of the species in which they occur.

There have been numerous confusions between galls and the lateral 'polysporangia'. The figure of *Gongroceras agardhianum* given by Kützing (1862, pl. 77) has been a constant source of confusion. A study of the specimen on which this figure is based (now in the Rijksherbarium, Leiden) proves beyond doubt that the structures illustrated by Kützing are galls, but the figure has been copied repeatedly by subsequent authors (Lakowitz, 1929, fig. 485; Kylin, 1937, fig. 117 D, 1956, fig. 28 D; Oltmanns, 1904, fig. 425.4, 1922, fig. 563.4; Schiller, 1913, fig. 1), the galls being described variously as 'polysporangia' or 'parasporangia'. The report by Phillips (1926) of the occurrence of 'parasporangia' in a specimen of *Ceramium* collected in Anglesey is also based upon a misinterpretation of galls, whilst it would appear that both van Goor (1923) and Feldmann-Mazoyer (1940) have made the same error in their interpretation of *C. deslongchampsii*. The figure of *C. tenuissimum* with 'parasporangia', given by Feldmann-Mazoyer (1940, fig. 113 p) is almost certainly based upon a gall.

It is to be regretted that the failure to detect any of these structures during extensive collecting of species of the genus *Ceramium*, undertaken throughout the British Isles during the last seven years, has prevented any detailed investigation of their structure, development and significance. In view of the many confusions between the galls and lateral 'polysporangia', the similarity between the few figures of the early stages of development of 'polysporangia' and the initiation of a gall and the lack of information on the development and germination of 'polyspores', the possibility that all supposed 'polysporangia' are nothing more than galls cannot be rejected.

The second type of structure, which consists of an irregularly shaped mass of spores, is formed only in an apical position. The first report of the occurrence of these structures was made by Kützing (1863, p. 1, pl. 1) in his account of *Hormoceras acrocarpum*, whilst Schiller (1913) has given a detailed account of their structure and development in *Ceramium strictum*. According to Schiller, the specimens occurred in an area of the Adriatic Sea where there was heavy pollution by sewage. Feldmann-Mazoyer (1940) has given a report of similar structures in *C. diaphanum*, but in the ecological notes she makes no mention of organic pollution. This type of structure does not appear to have been reported outside the Mediterranean. Nothing is known of the early stages of development, but the origin of the spore-masses by the modification of a tetrasporangium would appear to be very improbable. Schiller (1913, fig. 18) has given a figure of a young stage of germination of a spore from one of these spore-masses but the subsequent development of the germlings is unknown. Although nothing is known of their cytology or of their significance in relation to the life histories of the species in which they occur, the application of the term 'parasporangium' to these spore-masses would appear to be justified, pending a more detailed cytological and cultural investigation.

Finally, Richard (1901), in the original description of *Ceramothamnion codii* (= *Ceramium codii* (Richards) Mazoyer), described, in addition to male and tetrasporic plants, a third type of thallus in which occurred spore-masses of a type very different from those described by Schiller. The spore-masses of *Ceramium codii* are subtended when mature by a group of adventitious axes, and, because of this, they bear a close resemblance to carposporophytes. The early stages of development of these spore-masses (Richards, 1901, pl. 22, figs. 17, 18) are not very clear and Richards, in the absence of any indication of a carpogonium, regarded the spore-masses as 'polysporangia'. Collins & Hervey (1917, p. 134) admit that the supposed 'polysporangia' are 'quite indistinguishable from cystocarps' but state that the failure to detect the procarp is a strong argument against such an identification, although Howe (1918), commenting on the 'alleged polysporangia of non-sexual origin where one would naturally expect cystocarps of sexual origin', has suggested that the 'alleged polysporangia...are in reality cystocarps'. *C. codii* has been reported in the British Isles (Dixon, 1958), but only in a sterile condition, so that further investigation of the spore-masses, which is obviously desirable, has not been possible.

Petersen (1908, p. 14) comments briefly on the occurrence of 'monospores' in *C. diaphanum*, but the basis for this report is not at all clear. As Rosenvinge (1924, p. 374) has commented, the citation by Petersen of a figure by Gobi (1877, fig. 8) is particularly baffling. It must be admitted that Gobi's figure is not particularly well drawn, but the structures are described by him as 'Tetrasporen', and, as Rosenvinge has commented, the structures in question are tetrasporangia, the division of which is not shown.

Vegetative propagation

There is considerable experimental evidence in various species of *Ceramium* to show that new thalli can arise from detached fragments of the axes (Oltmanns, 1895; Massart, 1898; Tobler, 1906; Chemin, 1928). Rhizoids develop adventitiously from the cells of the cortical bands so that the fragment becomes attached to the substrate, and then new apices regenerate in the manner already described (see p. 341).

FUNGAL INFECTIONS

There are numerous records of fungal infections in species of *Ceramium*, but little is known of the occurrence of these fungi in the British Isles. The nomenclature adopted in the following account is based essentially on that of Sparrow (1943).

Eurychasmidium tumefaciens (Magnus) Sparrow. Magnus (1872, 1875) described and figured *Chytridium tumefaciens* occurring in the axes and rhizoids of *Ceramium acanthonotum* (= *C. shuttleworthianum*) and *C. flabelligerum*. Subsequently transferred to the genera *Olpidium* (Wright, 1879) and *Pleotrachelus* (Petersen, 1905), the species was ultimately made the type species of a new genus *Eurychasmidium*, by Sparrow (1936), because of the biflagellate zoospores. The organism studied by Sparrow occurred in the cells of the cortical band and in the apical cells of *Ceramium diaphanum*, but was absent from the rhizoids. It has been suggested subsequently by Feldmann & Feldmann (1956) that two distinct fungi had been confused by Magnus (1872, 1875) in his original description of *Chytridium tumefaciens*. According to these authors, one organism (that studied by Sparrow) was restricted to the apical cell and the cells of the cortical band, whilst the other occurred only in the rhizoids. The latter entity was described as a new species under the name *Olpidiopsis magnusii*. Because of possible confusion between these two organisms, previous reports of the occurrence of *Eurychasmidium tumefaciens* must be regarded with caution, but it would appear that there have been no reports of the occurrence of this species in the British Isles since the early Irish record of Wright (1879). This is surprising in view of the frequency with which it has been collected on various species of *Ceramium* from many different localities (Dixon, unpublished). The fungal thallus develops within a superficial cell of a cortical band, or in an apical cell. The infected cell increases in size so that it forms, on the surface of the thallus, a spherical or hemispherical protuberance, which is extremely prominent due to its highly refractive contents, its thick wall and its size (Fig. 5 E, F). Following infection of a cell of the cortical band, the development of adventitious lateral branches of unlimited growth was noted only in a few examples, but Sparrow (1936, 1943) comments that in the material of *C. diaphanum* examined by him, the development of adventitious lateral branches of unlimited growth, subsequent to infection, is of very frequent occurrence, and that, as a result, the axes of the host species have a characteristic 'bushy' appearance, which is a useful indication of the site of infection. Sparrow mentions the infection of the apical cell of the host species but states that this causes little hypertrophy. In the

British material examined, the infection of the apical cell occurred very frequently with considerable effect on the appearance of the host. Cessation of apical growth of the axes was followed, in most cases, by the development of adventitious lateral branches of unlimited growth, such as are formed whenever the apical cell of an axis is damaged or destroyed. Feldmann & Feldmann (1956) suggest that the sites of infection of *Eurychasmidium tumefaciens* and *Olpidiopsis magnusii* are quite distinct, but from a superficial examination of the British material collected personally it would appear that this suggestion may not be fully justified. A more detailed investigation of the two supposed species and their characteristics is obviously required.

Chytridium megastomum Sparrow. Described originally by Sparrow (1934) as a parasite on *Striaria attenuata*, this fungus was detected subsequently at Woods Hole (Sparrow, 1936) as a parasite on *Ceramium diaphanum*. There is no evidence of its occurrence in the British Isles.

Pontisma lagenidioides Petersen. This fungus is restricted to species of *Ceramium*, occurring usually in the axial cells or the innermost cells of the cortical bands. *Pontisma lagenidioides* is widely distributed, occurring in various species of *Ceramium*: Denmark (Petersen, 1905), in *C. rubrum*, *C. strictum* and *C. fruticulosum*; Sweden, Gullmar Fjord (Aleem, 1955), in *C. diaphanum*; Germany, Kiel Bay (Höhnk, 1940), in '*Ceramium* sp.'; France, Banyuls (Aleem, 1950), in *C. diaphanum*; France, Roscoff (Feldmann, 1954; Feldmann & Feldmann, 1956), in *C. tenuissimum*; U.S.A., Woods Hole (Sparrow, 1936), in *C. diaphanum*. According to Sparrow (1943), *Pontisma lagenidioides* is found most commonly in dead or decaying material. In the British Isles it has been detected on two occasions, in a decaying specimen of *Ceramium strictum* collected in the drift at Port Erin, Isle of Man, and in a specimen of *C. diaphanum* collected *in situ* by Dr J. A. Kitching, at Lough Ine, Ireland.

Rhizophidium discinctum Petersen. Described originally from Scandinavia on various Chlorophyta, this species was detected subsequently on *Ceramium diaphanum* maintained in a laboratory aquarium for several days (Sparrow, 1936). There is no evidence of its occurrence in the British Isles.

Thrausochytrium proliferum Sparrow. Described originally by Sparrow (1936), as a saprophyte in *Bryopsis plumosa* and *Ceramium diaphanum*, there are no indications of the occurrence of this species in the British Isles.

Chytridium polysiphoniae Cohn. Cohn (1865) described this fungus as a parasite on *Polysiphonia violacea*; subsequently it has been detected on various marine algae, including *Ceramium*: Denmark, in *C. rubrum*, *C. strictum* (see Petersen, 1905); *C. fruticulosum* (see Sparrow, 1934); U.S.A., Woods Hole (Sparrow, 1936), in *C. rubrum*. Specimens probably referable to this species have been detected in the British Isles (Dixon, unpublished) on other host species, but not on species of *Ceramium*. According to Sparrow (1943), *Chytridium polysiphoniae* is undoubtedly a 'composite' species in need of detailed investigation.

Petersenia pollagaster (Petersen) Sparrow. Reported originally in Denmark by Petersen (1905), in *Ceramium rubrum*, and again by Sparrow (1934) in '*Ceramium* sp.', it is very probable (teste Aleem, 1955) that this species is not distinct from *Petersenia lobata* (Petersen) Sparrow, which has been collected from a variety of host species in Denmark (Petersen, 1905; Sparrow, 1934), the United States (Sparrow, 1936) and Sweden (Aleem, 1955). Neither entity has been detected in the British Isles.

Olpidiopsis andreei (Lagerhaim) Sparrow. There is some doubt concerning the occurrence of this fungus in *Ceramium*. Sparrow (1934, 1936, 1943) has reported the occurrence of a '*Pleotrachelus*-like' fungus in *Ceramium diaphanum*, which is probably referable to *Olpidiopsis andreei*, whilst Aleem (1950) has identified as *O. andreei* a fungus collected in *Ceramium diaphanum* at Banyuls. As this species occurs most frequently in genera of the Chlorophyta and Phaeophyta, the reports of its occurrence in *Ceramium* should be treated with caution.

Olpidiopsis magnusii Feldmann & Feldmann. It has been suggested by Feldmann and Feldmann that the previous reports of *Eurychasmidium tumefaciens* refer to two different organisms (see p. 359). These authors have separated what they consider to be the two forms and have described *Olpidiopsis magnusii*, as occurring in the rhizoids of *Ceramium flabelligerum* at Roscoff (Feldmann, 1954; Feldmann & Feldmann, 1956). An organism similar to that described by these authors has been collected on two occasions in specimens of *C. flabelligerum*, but in addition to the infection of the rhizoids, cells of the cortical bands of these specimens were also infected, with the fungus similar to *Eurychasmidium tumefaciens*. Unfortunately, the specimens had been fixed before examination so that detailed study was impossible, but it is obvious that a detailed investigation of the two species and their supposed characteristics is urgently required.

Pythium marinum Sparrow. *P. marinum* was described originally bySparrow (1934), occurring saprophytically on *Ceramium rubrum* in Denmark. There is no indication for its occurrence in the British Isles.

Pythium maritimum Höhnk. Höhnk (1940) collected at Kiel a species of *Pythium*, growing saprophytically on '*Ceramium* sp.'. From the illustration given by Höhnk (1940, fig. 4) the host species cannot be determined with certainty, but it would appear to be a species of the *diaphanum*/*strictum* complex (sensu Feldmann-Mazoyer, 1940). Höhnk claimed that this species of *Pythium* differed in certain respects from *P. marinum* Sparrow and it was therefore described as a new species under the name *P. maritimum*. There are no reports of the occurrence of *P. maritimum* in the British Isles. The differences between *P. marinum* and *P. maritimum* do not appear to be very significant and it is to be regretted that an authoritative opinion as to the status of these two entities is not available, as the description of *P. maritimum* would appear to have been overlooked in the most recent monograph of the genus (Middleton, 1943).

Aleem (1955, p. 25) has given a brief account of an organism of uncertain affinity, found in the cortical cells of *Ceramium rubrum*, near Kristineberg, Sweden, which he compared with *Pyrrhosorus marinus*, described by Juel (1901) from material of *Cystoclonium purpureum* from the same area. The observations of Aleem are extremely brief, being based upon a single collection, and in view of the possible complexity of the life history of this organism, the report should be treated with caution until more detailed observations are available.

THE VALIDITY OF CRITERIA USED FOR SPECIFIC AND VARIETAL SEPARATION

At the present time, the taxonomy of the genus *Ceramium* is in a state of chaos. This is the result of the failure of phycologists to refer back at all times to original authentic material and the failure to recognize and interpret seasonal and environmental modifications of the external form of the thallus. The search for nomenclatural type specimens is frequently a long and laborious task but, with patience, it is usually possible to locate the authentic material. In order to overcome the second difficulty, the value of the features used for the separation of species must be assessed critically. Frequently, the characters by which different supposed taxa are reputedly distinguished prove on detailed examination to have no real significance. It is obvious that a critical survey of the validity of the criteria used for specific and varietal separation is essential if these difficulties are to be overcome.

The morphological features used by previous authors for the separation of species and varieties in the genus *Ceramium* are as follows: (1) the number of pericentral cells, (2) the development of the cortical band, (3) the dimensions of the axial cells, (4) the 'index of cortication', (5) the occurrence of adventitious lateral branches of unlimited growth, (6) the distance between pseudo-dichotomies, (7) the curvature of the apices, (8) the spines. Each of these morphological features will now be discussed in detail.

The number of pericentral cells

From four to ten pericentral cells are formed from each segment of the apical cell of an axis of unlimited growth. The number of pericentral cells produced varies from species to species, but it is relatively constant for each species. This feature has been used by some previous investigators, but it must be applied with care, because of the slight variation which does occur. A species with seven pericentral cells, where segments with six and eight pericentral cells occur occasionally, can be distinguished readily from a second species where four pericentral cells occur constantly.

As Phillips (1926) has stated, the number of pericentral cells can be estimated accurately only by tracing the pit-connexions with the axial cell. Usually the number of pericentral cells can be counted in a transverse section with a fair degree of accuracy, even if the pit-connexions are not located, but in old material errors may be introduced by this technique, as it is possible for a cell derived from a pericentral cell to intercalate itself into the ring of pericentral cells. Although the pericentral cells are often visible in a side-view of an axis, attempts to count them in this position are unlikely to be successful, particularly with the larger numbers.

The development of the cortical band

The appearance of the cortical band is the principal diagnostic feature in the genus *Ceramium*. Despite its importance, there have been no critical studies of the features controlling the development of the band and little regard for the modifying effects of season and environment. The different types of cortical construction exhibited by the various species of *Ceramium* can all be related to the patterns of cell division and cell enlargement occurring in the branches of limited and unlimited growth. The cortical band itself may be regarded as a cylindrical structure formed by the aggregation of the filaments of limited growth which are orientated radially as well as acropetally and basipetally.

The radial dimensions of the cortical band are determined by the degree of enlargement of the pericentral cells and their immediate derivatives, together with the extent of growth of the radially orientated filaments of limited growth. Of these two factors the former is by far the more important. The enlargement of the pericentral cells and their immediate derivatives occurs quite independently of the enlargement of the axial cells. As a result, the outline of the axes may be regularly cylindrical if the enlargement of the axial cells and the radial growth of the cortical band is balanced, or the axes may be constricted or inflated at the cortical bands if there is any marked difference between the enlargement of the one and the radial growth of the other.

The length of the cortical band produced at each segment of an axis is determined by two factors: (1) the number of divisions of the apical cells of the lateral branches of limited growth, (2) the degree of enlargement of the cells of the lateral branches of limited growth. Variation in the length of the cortical band results from variation of one or both of these factors.

In certain species, the apical cells of the lateral branches of limited growth may cease to divide at a very early stage of development, so that any increase in the length of the cortical band is caused entirely by increase in cell size. This is in fact relatively restricted, so that in these species there is very little variation in the dimensions of the cortical bands as the thallus ages. In those species where the apical cells of the lateral branches of limited growth continue to divide throughout the life of the thallus, there may be considerable variation in the dimensions of the cortical bands. Where the apical cells of the lateral branches of limited growth continue to divide throughout the life of the thallus, the acropetal and basipetal margins of the cortical bands are either sharply defined and parallel to one another (Fig. 3 G) or very diffuse and ill-defined (Fig. 3 H), according to whether the divisions of the apical cells take place synchronously or irregularly. Finally there may be marked differences between the growth of the acropetal and basipetal faces of a cortical band resulting from differences in the rates of cell division and cell enlargement.

It should be noted that in those species where the cortex forms a continuous investment to the axial filament, it is often difficult to ascertain the limits of the cortical bands as the lateral branches of limited growth of adjacent segments merge with one another.

In conclusion it may be stated that the appearance of the cortical band is perfectly adequate as a diagnostic character, providing that the patterns of cell division and cell enlargement are interpreted correctly.

The dimensions of the axial cells

An axial cell is derived from each segment of a principal apical cell; after the formation of pericentral cells, no further divisions occur and the resulting axial cell merely increases in size. The ultimate dimensions of an axial cell are determined by its position in the thallus and the pattern of cell enlargement is extremely complex. The dimensions of the axial cells are of obvious importance in that they determine the dimensions of the frond. In order to investigate the pattern of cell-size variation, measurements were made of every axial cell in plants of various species collected from a wide range of environments from different parts of the British Isles. Although there are considerable fluctuations in the dimensions of the axial cells, both between species, and even in the same species, the same general pattern of variation was detected in all the thalli examined.

The over-all range of size of the axial cells is shown by a comparison of the average length and volume of these cells in successive sectors of the thallus, from base to apex. In this connexion, the term 'sector' is applied to the portion of the thallus between successive 'dichotomies'. If the average length of the axial cells in each sector is calculated, the average length per sector increases from a minimum value immediately behind an apex to reach a maximum value either at or near the base of the thallus. The rate of increase of the average length of the axial cells per sector and the maximum value attained vary enormously and it is obvious that they are affected to a very great extent by the environmental conditions. The average measurements of the axial cells of the basal, first-formed, sectors of a plant are often slightly lower than the maximum size, but this decrease in size does not occur in all examples.

Measurements of the average size of the axial cell per sector, made in this way, do not show the very characteristic pattern of variation of cell-size within each sector. In any sector of the thallus, apart from those sectors immediately behind the principal apical cells, where *all* axial cells are enlarging actively, the axial cells show considerable variation in length, the smallest axial cell occurring at the basal end of the sector, that is, immediately after a 'dichotomy', whilst the largest occurs towards the opposite end of the sector (Fig. 14). In mature thalli, the largest axial cell in a sector is about twice the length, or about three times the volume of the smallest. This pattern of variation is complicated by other factors, for instance, the formation of tetrasporangia or the development of adventitious lateral branches of unlimited growth may inhibit to a certain extent the enlargement of the associated axial cell. As a result, there may be small irregularities in the pattern of axial cell size, but these have no major effects on the general pattern of variation within each sector.

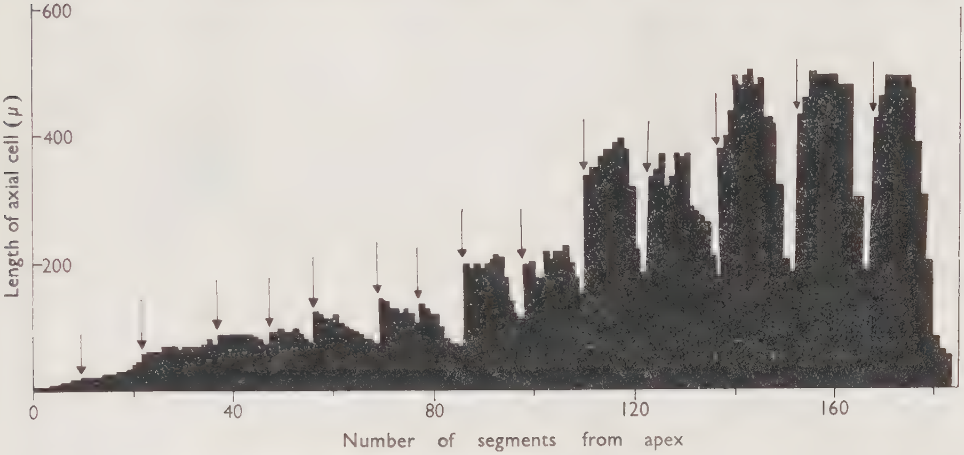

Fig. 14. Histogram showing the pattern of variation in size of the axial cells in relation to distance from the apex and the positions of pseudo-dichotomies; the position of each pseudo-dichotomy is indicated by an arrow.

The interaction of the two patterns of variation of axial cell size, that is, between the sectors of a thallus and within each individual sector, is most complex (Fig. 14). It will be obvious from this that any measurements of axial cell size must be cited in relation to a particular part of a thallus, and that 'average' measurements must be based upon sufficiently large samples (>300 cells).

The 'index of cortication'

In those species where the axes are incompletely corticated, the ratio of the length of the cortical band to the length of the adjacent non-corticated portion of the axial cell has been used as a taxonomic criterion.

Those investigators who have used this ratio do not appear to have given any consideration to the significance of this feature. As has been shown previously, the factors affecting the length of the cortical band are very complex, whilst the patterns of variation of axial cell size are extremely complicated.

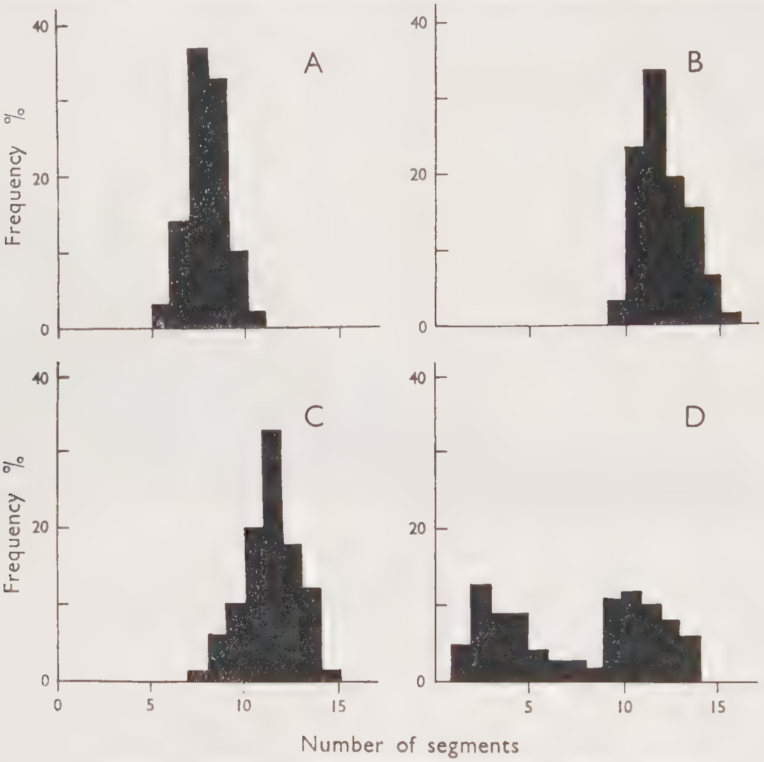

Fig. 15. A–D, Histograms showing the number of segments produced between successive pseudo-dichotomies in three species of *Ceramium*. A, *C. shuttleworthianum*; B, *C. echionotum*; C, *C. ciliatum*, excluding adventitious lateral branches; D, *C. ciliatum*, including these branches.

Furthermore, the 'index of cortication' does not represent the direct ratio of the dimensions of the cortical band and the axial cell, as the length of the non-corticated portion of the axial cell is actually the *difference* of the lengths of the axial cell and cortical band. Hence, the 'index of cortication' may be represented as follows:

$$\text{Index of cortication} = \frac{\text{length of axial cell non-corticated}}{\text{length of cortical band}}$$

$$= \frac{(\text{length of axial cell}) \text{ minus } (\text{length of cortical band})}{\text{length of cortical band}}$$

$$= \frac{\text{length of axial cell}}{\text{length of cortical band}} - 1.$$

The interaction of the two patterns of variation is so very complex that significant differences in the 'index of cortication' occur in the same species, or even in the same specimen, according to the position on the thallus at which measurements are taken. As a taxonomic criterion, the 'index of cortication' is of very dubious validity.

The occurrence of adventitious lateral branches of unlimited growth

The formation of adventitious lateral branches of unlimited growth has been described previously (see p. 341), but no explanation can be offerred to account for the occurrence of these structures. Although most frequent in damaged specimens, they may develop prolifically in axes which are apparently normal. Adventitious lateral branches of unlimited growth are formed also in tetrasporic and 'cystocarpic' specimens after the shedding of spores has commenced and immediately beneath a developing carposporophyte. Although used frequently by previous investigators, the occurrence of adventitious lateral branches of unlimited growth is of very little taxonomic significance.

The distance between pseudo-dichotomies

In certain members of the Ceramiaceae, the formation of lateral branches of unlimited growth takes place with some regularity (cf. Chadefaud, 1954), but there is considerable variation in the genus *Ceramium* in the number of segments produced between successive pseudo-dichotomies. The measurement of the number of segments produced between successive pseudo-dichotomies (cf. Newton, 1931) is of very little significance even if the formation of adventitious lateral branches of unlimited growth is eliminated. If no distinction is made between lateral branches of unlimited growth of adventitious origin and those which have arisen by the pseudo-dichotomy of the apex, and in old specimens this is often impossible, the number of segments occurring between successive lateral branches has no taxonomic significance whatsoever.

The curvature of the apices

In some species of *Ceramium*, the apical portions of the axes are incurved strongly, whilst in others, the axes are straight throughout. The degree of curvature of the apical parts of the axes has been used by some previous investigators as a taxonomic criterion, particularly at the subspecific level.

The degree of curvature of the apical regions of an axis depends upon the relative rates of development of the lateral branches of limited growth in each segment. As stated previously, the first pericentral cell is formed in the secund position, that is, on the outer face of the axis relative to the previous pseudo-dichotomy. In those species in which the apices are strongly incurved, the apical cells of the lateral branches of limited growth are produced by the first-formed pericentral cell immediately after its formation. In this way, the cortical band is well established on the outer face of the axis by the time the final pericentral cell is cut off on the inner side (Fig. 1 D–F). As a result, when the final pericentral cell has been formed, each cortical band is wedge-shaped in longitudinal section, with the apices of the wedges pointing inwards, relative to the previous pseudo-dichotomy. The axes are formed by the aggregation of these wedge-shaped cortical bands and they are therefore strongly incurved. As the axes age, the eccentric development of the inner and outer faces of the cortical bands becomes less marked so that the degree of curvature diminishes until, in mature thalli, the axes are straight or almost so.

In those species of *Ceramium* in which the apices are straight or only very slightly incurved, the pericentral cells are cut off in rapid succession, and the further development of the filaments of limited growth does not take place until after the complete ring of cells has been formed (Fig. 1 A–C). The development of the cortical band is thus completely symmetrical in these species.

The degree of curvature of the apical region of an axis appears to be almost constant and is sufficiently stable to serve as a valid taxonomic criterion.

The spines

The comparative morphology of the spines in the British species of *Ceramium* has been discussed in detail (see p. 344). Although the spines of all the British species must be regarded as modified lateral branches of limited growth (Fig. 7 A–D), the spines are very different one from another, both in structure and development. Previous confusion with regard to the morphology of the spines is the result, essentially, of the failure to study the patterns of development by which spines are formed. In the European species, the patterns of development of the different types of spine are constant and sufficiently stable to serve as a valid taxonomic criterion.

DISTRIBUTION

According to Kylin (1956), there would appear to be about sixty species of *Ceramium*, of which twenty are reputed to occur in the British Isles (Parke, 1953). Such computations are of little significance as the taxonomy of *Ceramium* is in a chaotic state at the present time.

Much of this chaos has come about as a result of the failure to take notice of, and interpret, the modifying effects of season and environment upon exceedingly plastic material. The position has been made worse by the failure of many workers to refer back at all times to original or authentic material. As a result there have been numerous misidentifications, epithets have been misapplied by the majority of investigators and frequently the same entity has been described repeatedly under 'new' names by successive authors.

In this treatment of the genus *Ceramium* and its species, the determination of specific limits will be based entirely on morphological and ecological circumscription.

KEY TO THE BRITISH SPECIES

It is proposed to consider the British species of *Ceramium* in two groups. This treatment does not imply that the groupings are considered to be of fundamental importance; the species are arranged in this way merely for convenience.

Group A. Species in which the mature axes are either completely or incompletely corticate, but where the cortical bands give rise to spines.

Group B. Species in which the mature axes are either completely or incompletely corticate, but where spines are absent.

KEY TO THE SPECIES OF GROUP A

1. Spines single-celled. *C. echionotum*
   Spines two-, three- or four-celled. **2**
2. Each spine consisting of a linear row of cells, sharply delimited from the cortical band. **3**
   Each spine multicellular at the base, merging with the cortical band. *C. shuttleworthianum*
3. Basal cell of spine large (> 30 μ in length), hyaline or faintly pigmented. Spines usually in whorls, very conspicuous. Pericentral cells 6 or more. *C. ciliatum*
   Basal cell of spine less than 25 μ in length, deeply pigmented. Spines sparse, inconspicuous. Pericentral cells 4. *C. flabelligerum*

Note. A key to the species of group B is in preparation.

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STUDIES ON MARINE ALGAE OF THE BRITISH ISLES: *CERAMIUM SHUTTLEWORTHIANUM* (KÜTZ.) SILVA

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(Text-figs. 1–7)

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ORIGINAL DESCRIPTION

The species was first distinguished by Carmichael, as *Ceramium acanthonotum*, in his unpublished *Algae Appinensis*, the manuscript of which is now preserved at the Herbarium of the Royal Botanic Gardens, Kew. Harvey (in Hooker, 1833), in publishing Carmichael's description, regarded the species merely as a variety of *C. ciliatum*. Agardh (1844) raised the variety to specific status, and it is as *C. acanthonotum* that the species has been known generally. Kützing (1841),[1] in a revision of the genus *Ceramium*, had described the entity independently as *Acanthoceras shuttleworthianum*; the specific epithet *shuttleworthianum* has priority over *acanthonotum* [see Article 60 of the International Code of Botanical Nomenclature (Lanjouw, 1956)]. The priority of the epithet *shuttleworthianum* was indicated, independently, by both Silva (1959) and Dixon (1959); of the two publications, that by Silva is the earlier.

The original material of *A. shuttleworthianum* is preserved at the Rijksherbarium, Leiden. According to Kützing (1841, p. 739), the species was described on the basis of material 'an der irischen Küsten: Shuttleworth'. In the Kützing herbarium there is a single Irish specimen of *A. shuttleworthianum* attached to a small mussel (*Mytilus*);

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[1] For comments as to the precise date of publication, see Dixon (1960, p. 333)

this has been designated as the type specimen (Herb. Lugd. Bat. 940.265.127). The specimen is labelled only as 'Irland' and no further information is available as to the locality from which it was collected.

SYNONYMY

Ceramium ciliatum β acanthonotum Carm. ex. Harv. (in Hooker, 1833, p. 236).
Ceramium acanthonotum (Carm. ex Harv.) J. Agardh (1844, p. 26).

For details of the type material of this entity, see Appendix (p. 388).

DESCRIPTION OF THE SPECIES

Frond lax, 0·5–4·0 cm in length, red or reddish brown in colour; axes filiform, 0·1–1·0 mm. broad, usually entangled or intertwined; branching regularly pseudo-dichotomous in the apical region, highly irregular in the older parts due to damage and subsequent regeneration by the development of adventitious lateral branches of unlimited growth; cortex bearing spines; cortical bands always distinct, even in the apical region; spines conical, secund or in whorls, multicellular at the base; cells of spine small ($< 25\,\mu$ diameter) with pigmented chromatophores.

Tetrasporangia secund or in whorls, emergent from the cortical band when mature.

Spermatangia forming colourless patches over each cortical band.

Carposporophytes spherical, usually lateral, sessile, subtended when mature by a single adventitious lateral branch of unlimited growth.

STRUCTURE AND DEVELOPMENT OF THE THALLUS

The principal apical cells of the axes of *Ceramium shuttleworthianum* are smaller than those of most other species of *Ceramium*, but the pattern of segmentation conforms to the general description already given (Dixon, 1960).

Each segment cut off by the principal apical cells of an axis gives rise to four pericentral cells (Figs. 1E, 2H–K). There is no variation in the number of pericentral cells produced. The filaments of limited growth arise from the pericentral cells, and their development is restricted so that the length of the cortical bands rarely exceeds $120\,\mu$ (Fig. 3A–C). The enlargement of the axial cells varies enormously, so that the 'index of cortication' is extremely variable. Kützing (1862, p. 29) described *Acanthoceras shuttleworthianum β longiarticulatum*, characterized by the extreme length of the non-corticated axial cells in mature parts of the thallus. The taxonomic status of this entity will be discussed later.

From six to ten segments are produced by the principal apical cells between each pseudo-dichotomy. Mature thalli of this species are of very irregular appearance and only rarely do they exhibit the characteristic pseudo-dichotomous structure found in other species of the genus. Most specimens suffer severe damage either by animal grazing or as a result of the extreme exposure of the environment in which they occur. In addition, infection of the principal apical cells of the axes by *Eurychasmidium tumefaciens* (see p. 383) occurs frequently (Fig. 6A). The subsequent regeneration of adventitious lateral branches of unlimited growth (Fig. 1 D) results in a tangled mass of irregularly branched axes.

Glandular cells occur frequently in *Ceramium shuttleworthianum*, although not reported in this species by previous investigators. Development occurs as in other species of the genus, by the direct modification of a superficial cell of the thallus.

The spines of *C. shuttleworthianum* are of very characteristic appearance. During the formation of a spine (Fig. 2 A–K), the apical cell of a lateral branch of limited growth divides rapidly to form a projecting filament of

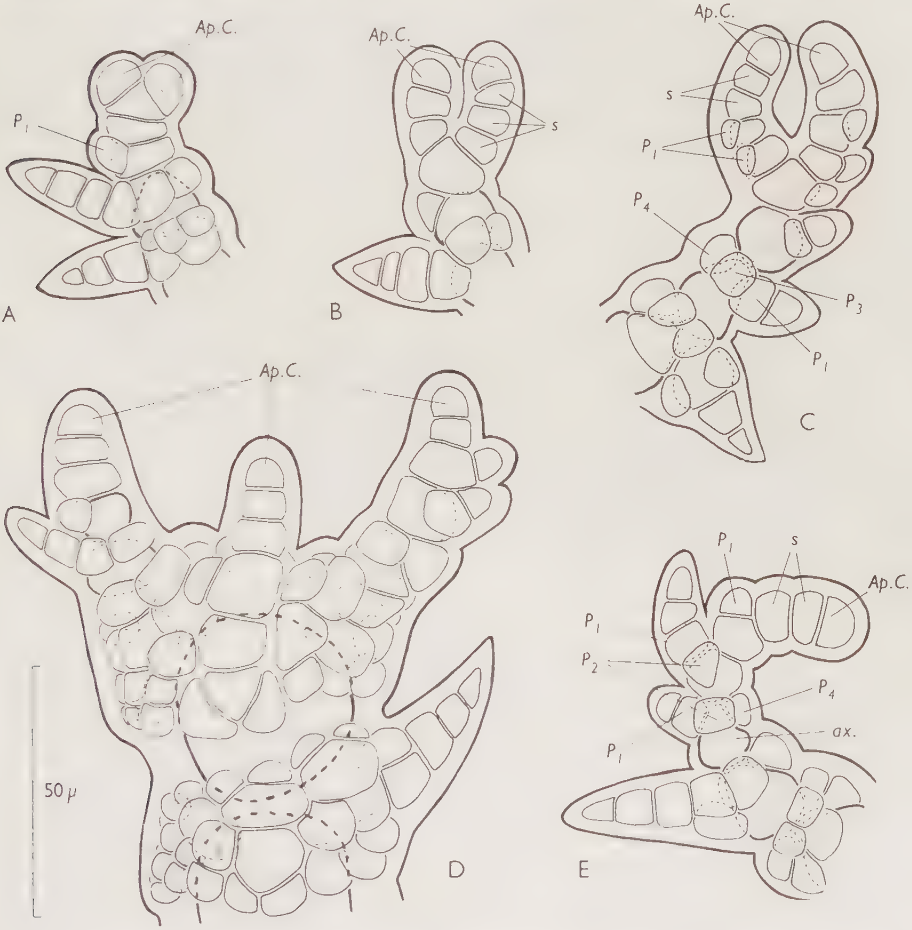

Fig. 1. The apex and the origin of lateral branches of unlimited growth in *C. shuttleworthianum*. A–C, Pseudo-dichotomy of the apex; D, origin of adventitious lateral branches of unlimited growth in a damaged axis; E, the apex of an axis, showing the general pattern of segmentation. *Ap.C.*, apical cell of an axis; *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; *s.*, segment, produced by the transverse division of the apical cell of an axis.

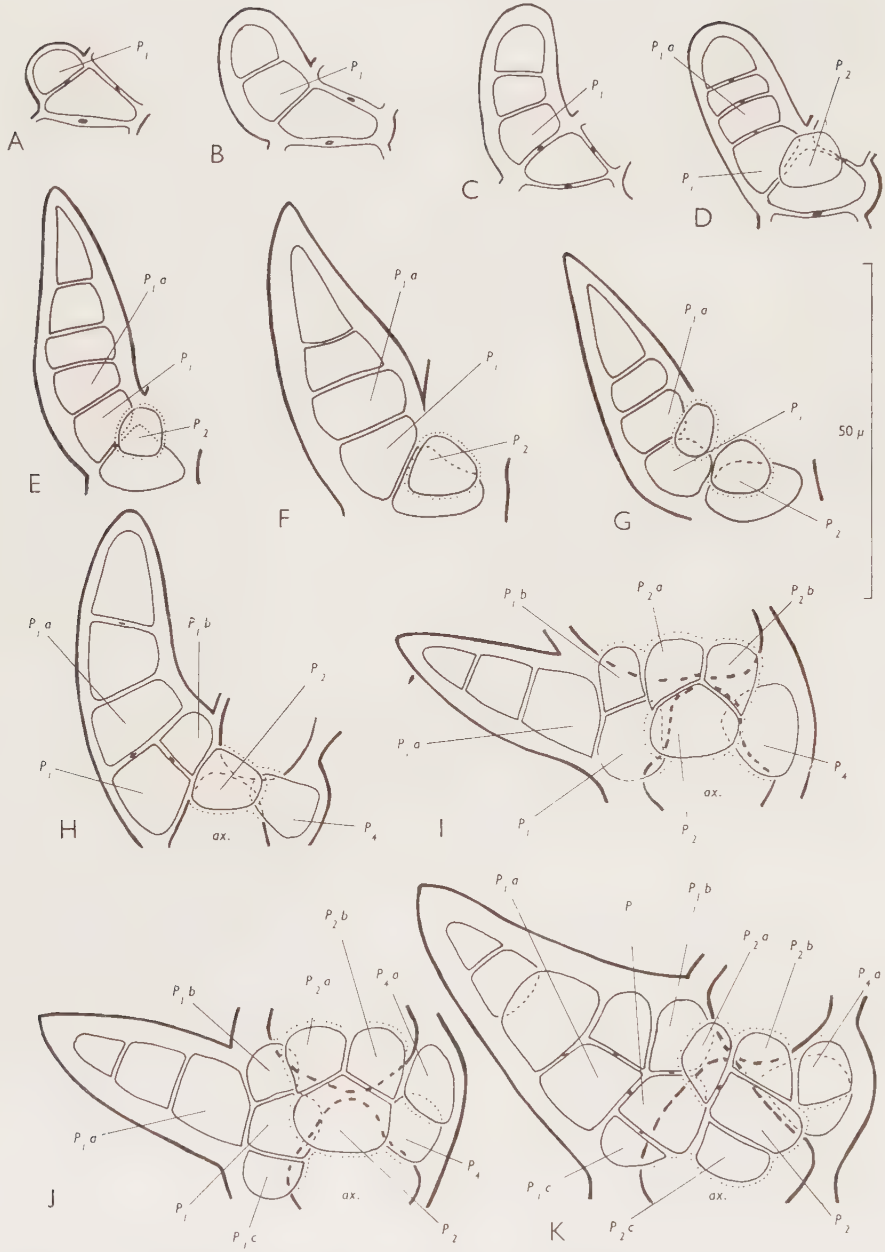
A
B
C
D
E
F
G
H
I
J
K
P_1
P_1a
P_1b
P_1c
P_2
P_2a
P_2b
P_2c
P_4
P_4a
P
ax.
50 μ

Fig. 2. A–K, Details of the stages in the development of the cortical band, in *C. shuttleworthianum*. *ax.*, axial cell; P_1, P_2, etc., pericentral cells, numbered in order of formation; P_1a, P_1b, acropetally-directed apical cells of lateral branches of limited growth, produced from P_1; P_1c, P_1d, basipetally directed apical cells of lateral branches of limited growth, produced from P_1, etc.

three to five cells. The rapid development of the spines is indicated by the occurrence of fully developed spines within one or two segments of the apex of an axis. The lowermost cells of the filament divide transversely to form part of the cortical band, whilst the other cells of the filament, that is, those cells which project to form the spine, may divide transversely also, so that the spine is conical in shape, with a broad multicellular base. The cells of the spine do not enlarge excessively, as in some other spine-bearing species of *Ceramium*. Moreover, the chromatophores and cytoplasmic contents are retained so that the cells of the spine resemble the cells of the cortical bands. As a result, the boundary between spine and cortical band is not sharply defined, as in many of the spine-bearing species of *Ceramium*, and the spines merge with the cortical bands in *C. shuttleworthianum* (Fig. 3).

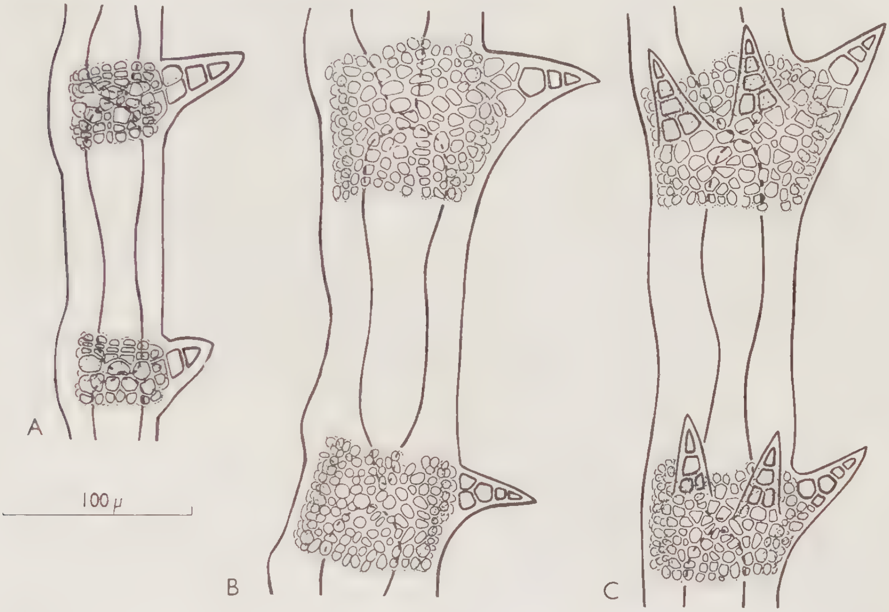

Fig. 3. A–C, Range of form of the axes in *C. shuttleworthianum*.

Adventitious spines may develop occasionally from the cortical bands of old mature axes. Such spines, which resemble the primary spines in appearance, occur most frequently in specimens which have been grazed by animals or damaged in some other way.

The number of spines occurring at each cortical band is not constant. In every cortical band, a single spine is formed in relation to the first pericentral cell, but other spines may develop in relation to the other pericentral cells, or arise in an adventitious manner. In the extreme case, a whorled arrangement of spines may result (= var. *coronata* Kleen, 1874). The taxonomic significance of these observations will be discussed later (see p. 386).

The life-span of the thalli of *C. shuttleworthianum* is extremely variable. At certain localities in the west of Ireland it would appear that many of the thalli are perennial; Boney (unpublished data) has reported the perennation of large thalli in south Devon. From herbarium collections, it is obvious that in France thalli can survive through the winter. In northern England and Wales, on the other hand, the erect system of the thallus survives only rarely for more than one season. At Porth-tre-Castell (Anglesey), in the case of plants growing on smooth rock, new thalli arise in the early spring (March–April) and die back completely in the late autumn and early winter (October–December). No evidence of the survival of the basal portions of these thalli through the winter could be obtained, but in other localities the thalli do not disappear completely. The formation of new erect fronds in the spring from fragments of the basal portions of thalli which have persisted through the winter has been detected in specimens growing in crevices in rock or concrete, or on rotten wood. It has not been possible to determine whether this process can be repeated indefinitely, but this would appear very probable. In south Devon, according to Boney (unpublished data) perennation of small fragments in rock crevices occurs on shores exposed to heavy wave action, whilst on more sheltered shores, with fucoid cover, whole thalli may overwinter as small tufts, 0·5–2·0 cm high.

STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS AND CARPOSPOROPHYTE

The tetrasporangia of *C. shuttleworthianum* are produced in the cortical bands (Fig. 4C). The number of tetrasporangia formed in a given cortical band varies considerably. In many specimens, only a single tetrasporangium develops in each band, on the outer side of the axis relative to the previous pseudo-dichotomy. Frequently several tetrasporangia develop in each band, and in the extreme condition a whorled arrangement results. The mature tetrasporangia measure 50–100 × 20–40 μ and when fully developed they are usually only partially immersed in the cortical band (Fig. 4C). The cortical bands of *C. shuttleworthianum* are relatively small and the internal development of the tetrasporangia causes extensive distortion, so that the orientation of the spines is changed considerably.

Spermatangia are produced superficially from mother-cells derived from the apical cells of the lateral branches of limited growth. Frequently the whole surface of the cortical band is covered with spermatangia (Fig. 4B) and when a large number of cortical bands is involved then the thallus develops a very characteristic indefinite outline which is readily identifiable.

No detailed studies have been made previously of the structure and development of the carpogonial branch and carposporophyte of *C. shuttleworthianum*, although Miranda (1929*b*) has stated that the carpogonial branch and carposporophyte resemble those of *C. flabelligerum* (Miranda, 1929*a*). Despite the abundance of carposporophytic material of *C. shuttleworthianum* in Ireland, the Channel Islands and the Isle of Man, the collection of specimens of this species with carpogonial branches and young stages of carposporophyte development was found to be particularly difficult. In seven years, only a single suitable specimen was collected. From this one specimen it would appear that the carpogonial branch is of the characteristic four-celled structure and that the supporting cell is formed by the modification of a first-formed pericentral cell. The lack of suitable material has prevented any detailed study of the carposporophyte development. The mature carposporophyte is

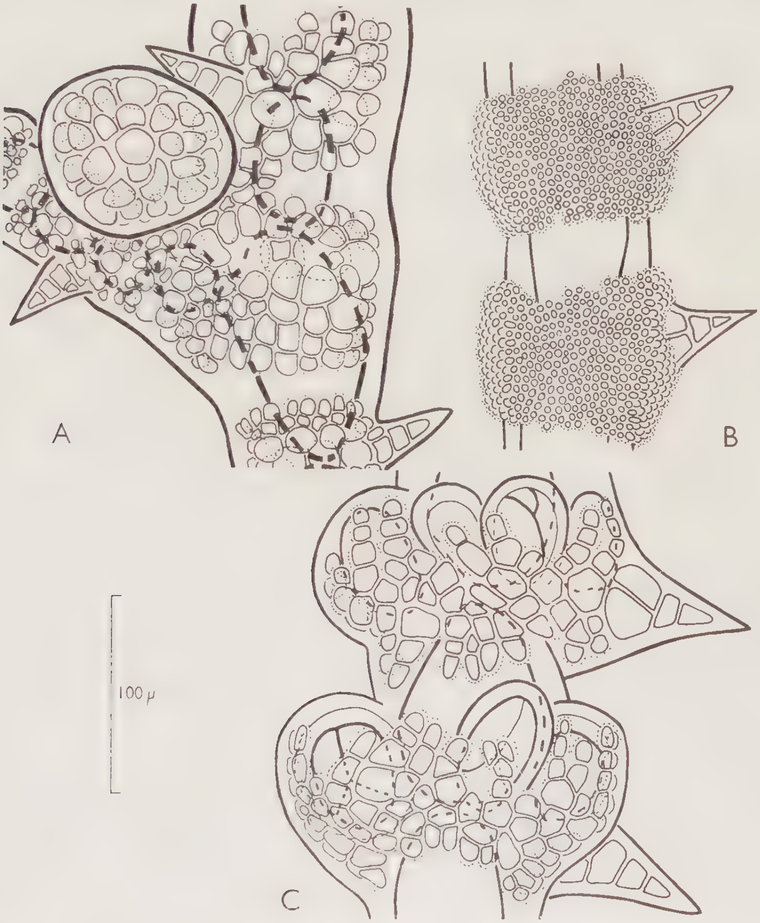

Fig. 4. A–C, Reproductive structures in *C. shuttleworthianum*.

typical (Fig. 7 A), but it differs from that of many other species of the genus in that it is subtended by only a single adventitious lateral branch of unlimited growth. In most species of *Ceramium* the mature carposporophyte is a lateral structure which is enveloped by a cluster of encircling adventitious axes, but in *C. shuttleworthianum* it appears to lie in a dichotomy of which one arm is formed by the parent axis and the other by the adventitious axis.

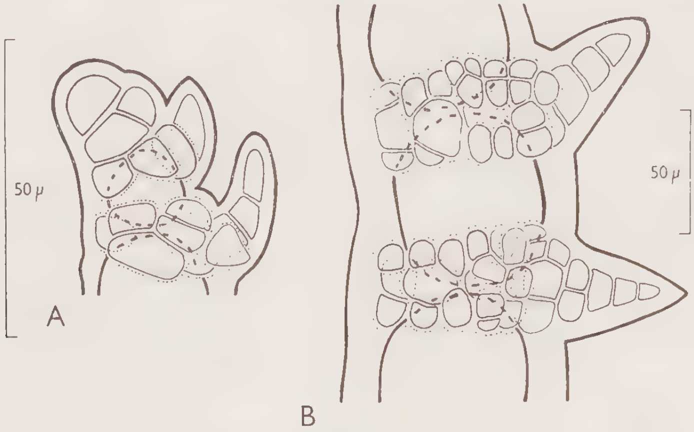

Fig. 5. A, B, *C. monacanthum*; drawings based on the type specimen (Herb. Alg. Agardh. 21162).

FUNGAL INFECTIONS

Numerous fungal infections have been reported in species of *Ceramium* (Dixon, 1960, p. 359). *Eurychasmidium tumefaciens*, described originally by Magnus (1872, 1875), and reported again by Wright (1879) in *Ceramium shuttleworthianum*, has been collected frequently, in that species of *Ceramium*, from a number of localities in the British Isles.

The principal apical cell of an axis is a frequent site of infection (Fig. 6 A); cessation of apical growth is followed by the development of adventitious axes. Infection of cells of the cortical band also occurs frequently (Fig. 6 B, C), but such infection is not followed by the development of adventitious lateral branches of unlimited growth, as was described by Sparrow (1936, 1943) in *C. diaphanum*.

DISTRIBUTION

Many previous records are incorrect because of confusion with other species of the genus. The following data are based upon examined specimens only.

British Isles

C. shuttleworthianum is generally distributed throughout the British Isles. Specimens from the following counties have been examined: Cornwall, Devon, Somerset, Dorset, Hampshire, Kent, Essex, York, Northumberland, Cumberland; Isle of Man; Glamorgan, Carmarthen, Pembroke, Cardigan, Merioneth, Caernarvon, Anglesey, Denbigh; Wigtown, Ayr, Bute, Renfrew, Argyll, Inverness, Ross and Cromarty, Sutherland, Caithness, Moray, Banff, Aberdeen, Fife, West Lothian, Midlothian, East Lothian, Berwick; Orkney, Shetland; Donegal, Sligo, Mayo, Galway, Clare, Kerry, Cork; Channel Islands.

Previous reports of the occurrence of this species in Norfolk, Durham and Cheshire have not been confirmed.

World

Iceland, Faroes, northern, central and southern Norway, and the Atlantic coast of France.

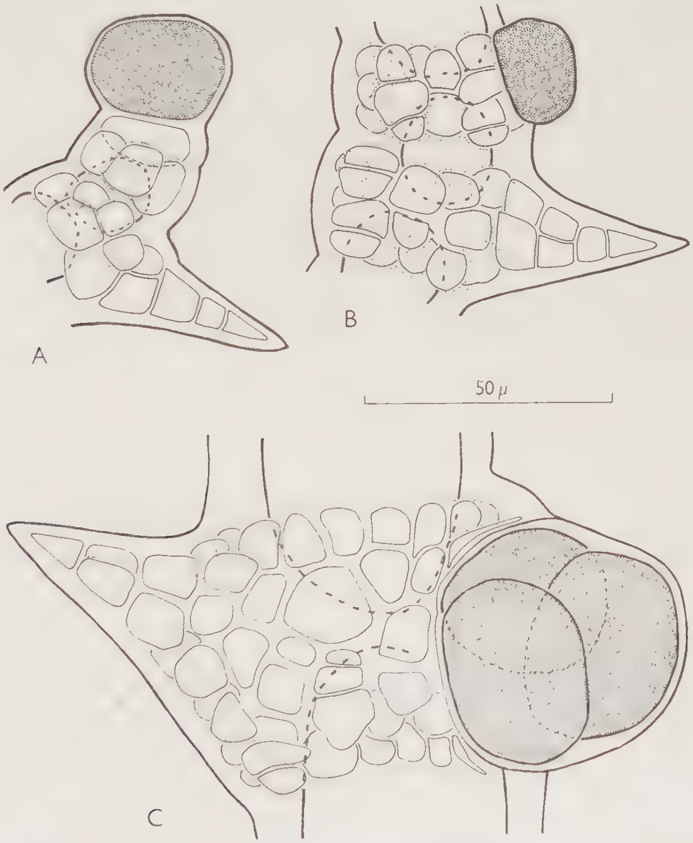

Fig. 6. A–C, Occurrence of *Eurychasmidium tumefaciens* in *C. shuttleworthianum*. A, Infection of the apical cell; B, infection of a cortical cell in a young cortical band; C, infection of a cortical cell in an old cortical band.

The southern limit of the species cannot be stated with certainty. Miranda (1929*b*) has claimed that the species occurs on the north coast of Spain, but this report must be treated with caution as no illustration is given by Miranda and it has not been possible to locate any specimens of *C. shuttleworthianum* from the area cited by this author. According to Børgesen (1930), the report of the occurrence of this species in the Canary Islands, by Sauvageau (1912, p. 184), is based on a misidentification; the specimens on re-examination proved to be a mixture of *C. ciliatum* and *C. flabelligerum*.

With regard to the northern limit of the species, it is obvious, from a study of the description and figure given by Sinova (1912), that the reported occurrence of this species in the Murmansk area is also based upon a misidentification.

It would appear that *C. shuttleworthianum* does not occur on the coasts of Germany (Migula, 1909) or Denmark (Rosenvinge, 1924), although it should be noted that Kützing (1845, p. 293) records the species from the island of Föhr, in the North Friesian archipelago. This record is based, according to Kützing, on a specimen collected by Frölich and identified by him as '*Ceramium diaphanum*'. This specimen is not in the Kützing herbarium at the present time and it would appear to be lost completely. The report of the occurrence of drift specimens of this species in Holland (Lucas, 1950) must be discounted, as it is the result of a misidentification (see p. 387).

Ceramium monacanthum[1] J. Agardh (1894, p. 29), from Tasmania (Fig. 5), bears a close resemblance to *C. shuttleworthianum*, but further studies of the former species are required before any pronouncements as to its status can be made.

HABITAT

C. shuttleworthianum occurs, under conditions of severe and moderate exposure, throughout the lower mid-littoral region. The species occurs on rock, or on *Mytilus*, *Balanus* and *Patella*, or on various species of algae. It is found only occasionally in pools.

REPRODUCTION

Tetrasporangia are formed normally from May to October. During the winter months, occasional plants collected in the west of Ireland have been found to be producing tetrasporangia in small numbers, whilst Boney (unpublished data) states that in south Devon a few tetrasporangia may be found during the winter, in the larger plants. Carpogonia and spermatangia are formed in May, June and July and carposporophytes are observable from June to December.

No detectable variation in the production of reproductive bodies in relation to tide level has been observed. With regard to latitude, sexual plants become increasingly rare in the northern parts of the British Isles and there do not appear to be any collections of sexual plants made to the north of Argyll on the west coast and Berwick on the east. Tetrasporic plants only are reported from Iceland, Norway and the Faroes.

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[1] For details of the type specimen, see Appendix.

LIFE HISTORY

Little is known of the life history of *C. shuttleworthianum.* From personal observations, equal proportions of sexual and tetrasporic plants have been detected in a number of localities on the west coast of Ireland, southern England and the Channel Islands, although, in the same locality, variations in the proportions of sexual and tetrasporic plants have been noticed from year to year. The observations of Boney (unpublished data) in south Devon, on the other hand, indicate a preponderance of tetrasporic plants in that region. In north Wales, northern England, the Isle of Man and parts of Scotland sexual plants are relatively rare, whilst they are unknown in northern Scotland, Norway, Faroes and Iceland. The occurrence of sexual and tetrasporic plants in equal proportions suggests that the life history is of the '*Polysiphonia*-type', with a regular alternation of sexual, carposporic and tetrasporic phases, but from the data presented above it would appear very probable that the sequence of phases in the life history may vary considerably over the range of the species.

The regeneration of new thalli from small fragments of the basal portions of old thalli of *C. shuttleworthianum* has been demonstrated. In certain localities, such regeneration occurs frequently, whilst in others it would appear to be relatively rare. The occasional occurrence of extensive perennation in any locality could have a profound effect upon the frequency of occurrence of sexual and tetrasporic phases, in that it could obscure the actual sequence of phases in a life history, or introduce deviations from the proportions of sexual and tetrasporic phases to be expected in a life history of the '*Polysiphonia*-type'.

FORM RANGE

Ceramium shuttleworthianum is one of the least polymorphic species of the genus. In the British Isles the dimensions of the thalli vary considerably, but the variation appears to result more from the effects of damage and the subsequent regeneration than from any other cause, although the degree of enlargement of the axial cells has some effect upon the size of the thallus. The species occurs throughout the lower mid-littoral region, but there is no detectable range of form in relation to tide level and it would appear very probable that this results from the extensive damage, which occurs at all levels, obscuring any effect of tide level on the form of the thallus. The species is found in pools only rarely. The specimens from pools are larger and more regularly branched than other specimens growing out of water at the same tide level.

Most specimens of *C. shuttleworthianum* collected in the British Isles develop a single spine at each cortical band (Fig. 3A, B), but occasionally a number of spines occur, forming a partial or complete whorl (Fig. 3C).

Kleen (1874, p. 19) proposed that such specimens should be separated as *C. acanthonotum* var. *coronata*. Kjellman (1883, p. 172), after a re-examination of Kleen's original material,[1] reduced the status of this variety to forma *coronata*, with the following remarks: 'In Kleen's collections only the typical form of *Ceramium acanthonotum* is to be found, but some specimens have the spines in certain parts of the frond so arranged as in the variety distinguished by Kleen. This variety resembling the typical form in all respects...it may be considered as rather little independent, though it deserves perhaps to be specially mentioned.'

Specimens with the spines in whorls have been reported from Norway (Kleen, 1874; Foslie, 1894) and Faroes (Børgesen, 1902), but apparently not from Iceland (Jónsson, 1902). From the literature it might appear that the number of spines formed at each cortical band is related to latitude. This opinion must be rejected for a number of reasons. First, over the whole range of the species there is little constancy in the number of spines produced, so that adjacent cortical bands in the same axis may bear a single spine or a whorl of spines; secondly, all intermediate states between the two extremes occur also, and thirdly, the whorled condition may result from the formation of a number of primary spines or from the subsequent development of secondary adventitious spines.

From this discussion it is obvious that there is no justification for the taxonomic separation of those thalli in which more than one spine is formed in each cortical band.

Kützing (1862) figured *Acanthoceras shuttleworthianum β longiarticulatum*, reputedly characterized by the extreme length of the axial cells in the mature parts of the thallus.[2] That there is no justification for the separation of *β longiarticulatum* is obvious, even from the original illustrations given by Kützing (1862, pl. 96, figs. a–f). Kützing gives a figure (pl. 96, fig. c) of the basal portions of *A. shuttleworthianum* and two figures (pl. 96, figs. e, f) of the basal portions of *A. shuttleworthianum β longiarticulatum*. Calculation of the 'index of cortication' for these three illustrations gives a mean value of 3·66 for *A. shuttleworthianum* and values of 1·25 and 4·25 for the two illustrations of *β longiarticulatum*. Examination of Kützing's original material of *β longiarticulatum* shows that the range of variation of the index of cortication in these specimens is from 0·75 to 5·0, which is not significantly different from the range in the species as a whole, based upon a series of measurements of a large number of specimens from a wide range of localities. There is thus no justification for the separation of this variety.

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[1] For comments on the type material of this variety, see Appendix.

[2] For a discussion of the type material and validity of publication of this entity, see Appendix.

THE INTERRELATIONSHIPS OF *CERAMIUM CILIATUM* AND *CERAMIUM SHUTTLEWORTHIANUM*

C. shuttleworthianum has been confused only with *C. ciliatum*. Harvey (in Hooker, 1833) regarded the species originally as a variety of *C. ciliatum* and this opinion has been repeated recently by Lucas (1950), who states: 'It is doubtful whether *C. acanthonotum* is a good species, for sometimes parts with whorls of spines and parts with spines on the outer side of the node only are found on the same plant.' It is obvious that a detailed study of the interrelationships of these two species is necessary if this confusion is to be overcome.

The two species were distinguished originally on the basis of spine distribution. It was supposed that in *C. ciliatum* the spines occur in whorls, whilst in *C. shuttleworthianum* a single spine occurs in each cortical band. From the previous discussion it is clear that more than one spine may occur in the cortical band of *C. shuttleworthianum*, whilst in *C. ciliatum*, although the spines occur frequently in whorls, there may be a reduction in the number of spines, so that in extreme cases only a single spine occurs at each cortical band. From this evidence it would appear that the separation of the two species is not justified. Careful investigation shows that this conclusion is incorrect, and that, although the *distribution* of spines is of little taxonomic significance, the two species are completely distinct.

In connexion with the opinions expressed by Lucas (1950), it should be noted that the re-examination of his material, now in the Rijksherbarium, Leiden, shows that the statement of this author as to the status of *C. shuttleworthianum* must be discounted, as none of the specimens identified by him as '*C. acanthonotum*' is of this entity; the specimens are of *C. ciliatum*, with a reduced number of spines.

The *morphology* of the spine is the most obvious character by which the two species can be distinguished. In *C. shuttleworthianum*, each spine is a conical structure, composed of from three to ten cells, two to four cells broad at the base (Fig. 3). The cells of the spine are of similar size (15–25 μ in diameter) and they retain their chromatophores and cytoplasm throughout the life of the plant. In *C. ciliatum*, the spine is formed of a uniseriate filament of three, or occasionally four or five, cells which differ markedly in size (Fig. 7). In mature three-celled spines the lowermost cell occupies more than half the length of the spine (30–50 $\mu \times$ 20–30 μ), the second cell is smaller (20–30 $\mu \times$ 10–20 μ), whilst the third cell is minute and triangular in shape. In four- and five-celled spines the differences in size between the cells of the spine are not so marked as in three-celled spines, but the lowermost cell is always the largest, whilst the terminal cell is always small and triangular. When first formed, the cells of the spine of *C. ciliatum* have dense cytoplasm and chromatophores, but as a result of the enormous increase in cell-size which takes place during development, the mature cells are frequently hyaline, although occasionally the remnants of cytoplasm and chromatophores may remain, forming curious patterns on the wall of the cell (see Feldmann-Mazoyer, 1940, fig. 55).

The two species may also be distinguished by the number of pericentral cells formed by each segment of a principal apical cell. Four pericentral cells are formed in *C. shuttleworthianum*, whilst six to eight are formed in *C. ciliatum*.

The two species can be distinguished, even in the field, by their size; with a good hand lens, the construction of the spine is clearly visible.

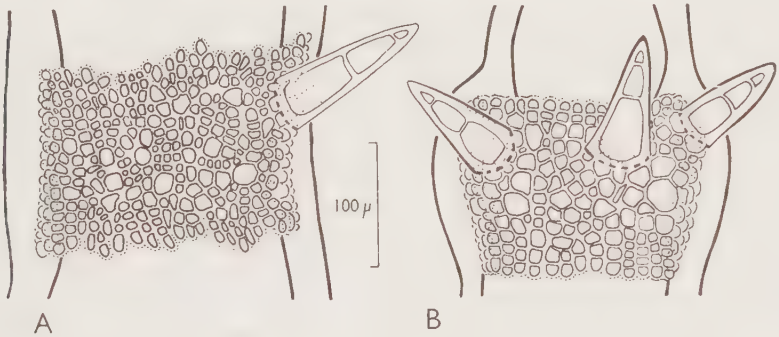

Fig. 7. A, B, Distribution of spines in *Ceramium ciliatum*.

APPENDIX

NOTES ON TYPE SPECIMENS

Acanthoceras shuttleworthianum β longiarticulatum Kützing, 1862, p. 29

Kützing's original reference to *A. shuttleworthianum β longiarticulatum* is extremely brief,

> '3076. *Acanthoceras Shuttleworthianum β longiarticulatum.*—Ad oras Angliae.'

but, as this is accompanied by an illustration (Kützing, 1862, pl. 96, figs. d–f) showing the essential characters, the name must be regarded as validly published [see Article 43 of the International Code of Botanical Nomenclature (Lanjouw, 1956)]. According to manuscript notes written by Kützing on a packet, containing four clumps of material, now in the Rijksherbarium, Leiden (Herb. Lugd. Bat. 940.265.154), the entity was based upon material collected by Dickie at Aberdeen. The four clumps of material are mounted on three pieces of card, each of which is labelled, in Dickie's hand, '*Ceramium acanthonotum* Carm Aberdeen Sept. 1845 GD'. A lectotype has been selected from the material available.

Location of lectotype: Rijksherbarium, Leiden (L), as Herb. Lugd. Bat. 940.265.154. Location of syntypes: as above. Locality of the type material: Aberdeen, Scotland.

Ceramium acanthonotum var. *coronata* Kleen, 1874, p. 19

It has not been possible to locate the original material of this variety, as the present location of Kleen's herbarium is unknown. It is obvious from the various comments made by Kjellman (1883) that he had examined numerous specimens from the Kleen herbarium, but no mention is made of the location of the herbarium. Only a single Kleen specimen of the species has been located, in the Rijksherbarium, Leiden (Herb. Lugd. Bat. 940.265.25). This specimen, labelled in Kleen's hand '*Cer acanthonotum* Carm Nordlanden', is from the same geographical area as the type material, but from the label it would not appear to be part of it. In the absence of type material, the illustrations given by Kleen (1874, Taf. 10, figs. 5*a*, *b*) are adequate for the purposes of identification.

Location of type specimen: unknown. Locality of type material: Nordlanden, Norway.

Ceramium ciliatum β acanthonotum Carm. ex Harv. in Hooker, 1833, p. 236

Several Carmichael specimens of *C. acanthonotum* have been located in herbaria. Neither Carmichael nor Harvey designated a holotype and no information can be obtained from the specimens, all of which are labelled, in Carmichael's hand, 'Carmichael H/A' (= 'Herbarium Appinensis'). A lectotype has been selected from the material available.

Location of lectotype: Herbarium, Royal Botanic Gardens, Kew (K). Location of syntypes: as above (2 specimens). Herbarium, Royal Botanic Garden, Edinburgh (E) (1 specimen). Locality of the type material: Appin, Argyle, Scotland.

Ceramium monacanthum J. Agardh, 1894, p. 29

The species was based on a single specimen collected by Roland Gunn in Tasmania.

Location of holotype: Botaniska Museet, Lund (LD), (as Herb. Alg. Agardh. 21162); Tasmania (no further details known).

ACKNOWLEDGEMENTS

I am indebted to Dr M. T. Martin for her encouragement and critical observations; to Prof. N. A. Burges, Dr E. M. Burrows and Dr M. W. Parke for advice and helpful criticism; to Dr A. D. Boney for permission to make use of unpublished data; to Mr R. Ross for assistance with nomenclatural matters and to Mrs Y. Butler, Miss C. I. Dickenson and Dr J. Th. Koster for help with literature and specimens. I would like to thank the Joint Committee on Research of the University of Liverpool for financial help towards the cost of visiting herbaria and libraries, and the Directors and Curators of the following herbaria for permission to examine specimens: British Museum (Natural History); Royal Botanic Gardens, Kew; Royal Botanic Garden, Edinburgh; Rijksherbarium, Leiden; Naturhistoriska Rijksmuseum, Stockholm; Museum Nationale d'Histoire Naturelle, Paris; Botaniska Museet, Lund.

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THE NEW AQUARIUM AND NEW SEA-WATER CIRCULATION SYSTEMS AT THE PLYMOUTH LABORATORY

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(Plates I and II, and Text-figs. 1–6)

Before describing the new aquarium some mention should be made of the final state of the old, which was described in detail some years ago (Wilson, 1952). Various suggestions for improvement made at that time were subsequently carried out. Thus the central table tanks were removed in 1953 and the central curtains, after shortening, were hung from the ceiling above the front top edge of the south-side tanks. This gave greatly improved viewing of the tank contents through exclusion of direct daylight to the public hall, and the viewing was still further improved when the south-side windows were blackened inside and the tanks lit solely by electric light. Modifications to the reservoirs (described below) brought about a clarity of the sea water never before attained.

The end came when the slate backs of several south-side tanks developed serious cracks, through which at one time water was pouring at over 70 gallons an hour and finding its way out of the building through ventilators in the south wall. No more than temporary repairs could be effected. The cracks resulted from the rusting of iron bolts pinning together the slate slabs of which the tanks were built. The bolt heads had been covered with slate dowels bedded in a red-lead compound which had kept the water back for nearly 70 years; it had at last penetrated to the bolts and expansion due to rusting cracked the slates.

The old aquarium was closed to the public for the last time on 27 September 1958 and demolition of the old tanks and fittings took most of October. It is of interest to record that the cast-iron window frames—which were moulded with the name of Leete, Edwards and Norman, London, a firm well known in Victorian days for its constructional work on big public aquaria—were in excellent condition and doubtless would have served for many more years. The condition of the iron tie-bars was on the whole also good, even in places where they had never been repainted and had a thick coating of rust, though here and there they had become dangerously thin. Much of the slate was in poor condition, splitting easily where rusting iron had cracked it and it would certainly not have held out much longer.

All the more valuable fish removed from the old tanks were, during the rebuilding, kept in tanks outside in the yard, or in the sea-water reservoirs, the water being kept in circulation. In the dimly lit reservoirs the fish flourished and grew, particularly *Pagellus*, *Spondyliosoma* and *Morone*. The *Polyprion*, mentioned in Wilson, 1953, p. 207, had a reservoir to itself and lengthened noticeably.

THE NEW AQUARIUM

Over many years various tentative plans for a new aquarium had been drawn and discarded. The necessity of erecting the new tanks within the existing tank room, where the central columns supporting the floors above must be retained, imposed severe limitations within which it was difficult to achieve a harmonious design pleasing to the viewer and at the same time providing greatly improved servicing facilities and a healthier environment for the animals. In the final plan these desiderata have largely been satisfied though at a cost of innumerable compromises. Thus, because of the restricted ceiling height the depth of water in the tanks is the maximum possible consistent with barely reasonable headroom over the cat-walks, and the latter have had to be kept several inches closer to the water surface than is desirable. Similarly the length and width of the tank room has influenced the shape of the tank windows, which are several inches shorter than they could otherwise have been. And so on throughout the whole structure.

In 1952 Garnaud suggested new shapes for aquarium tanks, until then almost always based on the rectangle. He proposed that the side walls should be built at 45° angles instead of at right angles. By so doing, triangular tanks alternate with others in which, owing to refraction and reflexion of light, the side walls cannot be seen through the windows when the tanks are full of water. This idea of angled-sides was adopted for the new aquarium at Plymouth, but modified from Garnaud's original scheme to accord with requirements within the available space.

In planning the aquarium the main objectives have been: (1) provision of the best possible conditions for the animals; (2) that as seen by the viewer each tank shall present as natural looking a scene as possible, well illuminated and with no 'works' showing; (3) ease of maintenance and day-to-day servicing. The first of these objectives has always taken precedence over the other two and the second almost always over the third. Only by so doing can a healthy and attractive aquarium be attained. In addition, the public hall and its approaches have been made as well proportioned and pleasing as possible.

The architect was Mr F. L. Preston, F.R.I.B.A., A.A.Dip., of Messrs Easton and Robertson, Cusdin, Preston and Smith, London, and the contractors Messrs John Garrett and Son Ltd, of Plymouth. The rockwork was designed and executed by Mr H. R. Allen, A.R.C.A., of Westerham, Kent.

Much technical help was given by members of the laboratory staff, especially Mr A. N. Bennett in the planning of the circulation system and Mr F. J. Warren in electrical fittings. Mr F. G. W. Ryder helped with many constructional details and overall supervision.

To all the above and others from whom I received assistance during the planning and construction of the new aquarium I wish to record my grateful thanks, and also to the Director, Dr F. S. Russell, F.R.S., for his continued support and encouragement.

The public hall

In the old aquarium[1] the tanks lined the north and south walls of the building and because they were wider on the north than on the south side the pillars occupied an asymmetrical position between them. By making the new north- and south-side tanks of equal width (see Text-fig. 1) these pillars are now centrally placed and one, the former easternmost pillar, has been removed to enable the largest tank to be constructed at the east end of the room. The weight of the floor above has been taken by two new concrete pillars merged with the central mullions of this tank. The public hall, as will be seen from the plan, widens at the east end. The new layout has in itself greatly enhanced the general appearance of the aquarium (Pl. I) and this has been further improved by an acoustically tiled ceiling with inset lights, hung below and concealing from public view the old vaulted ceiling and the unsightly overhead piping supplying tanks in the laboratory on the floor above. Underfoot a floor of dark red asphalt is a pleasing substitute for concrete with iron gratings. The public reach the aquarium along a partly reconstructed and newly decorated hall and passage and enter it through swing-doors and a small low-ceilinged lobby.

Wooden sides to the lobby, fluted and polished, are service doors which enable staff to cross it between north- and south-side service areas. These service areas, or short passages, are cut off from the public hall by a fluted polished screen of Afrormosia wood in which, to the north of the lobby, are three small angle-iron tanks, one below and two above, attractively framed in the screen (Text-fig. 2, section AB). In the south-east corner an emergency exit has been constructed utilizing one of the old window arches. A circular seat has recently been put around the pillar nearest the large tank.

On the sills in front of the tanks (Pl. I) frames of Afrormosia wood hold picture labels (lettered water-colour drawings sealed between Perspex). Each frame holds five labels which can be slid in from either end and screwed up against interference. A removable wooden hand-rail on iron supports inserted

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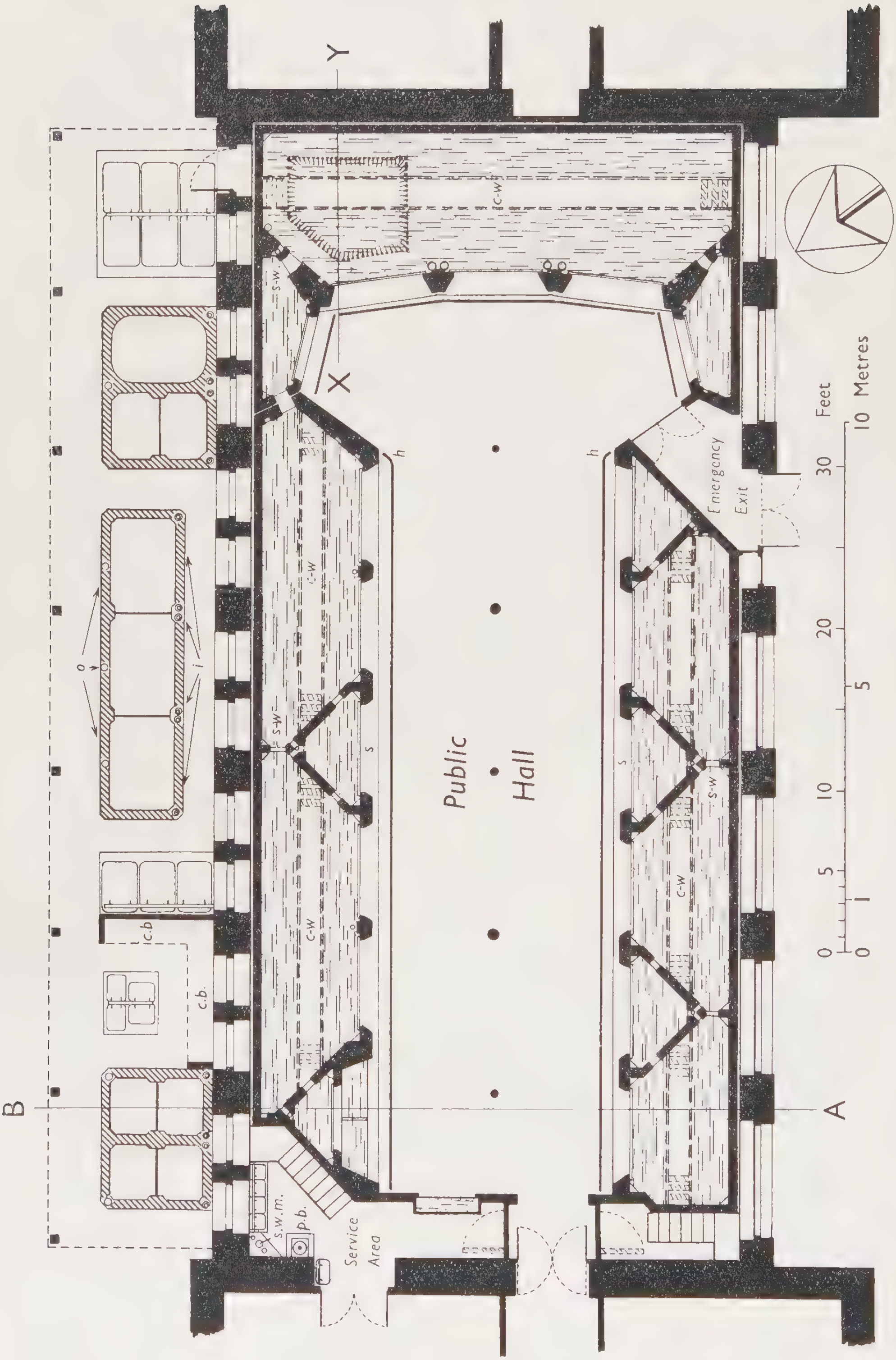
[1] Photographs of the old aquarium are reproduced in Allen & Harvey, 1928 (fig. 6), Russell, 1948 (pl. XXIII), and Wilson, 1952 (pl. I).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Text-fig. 1. For legend see facing page.

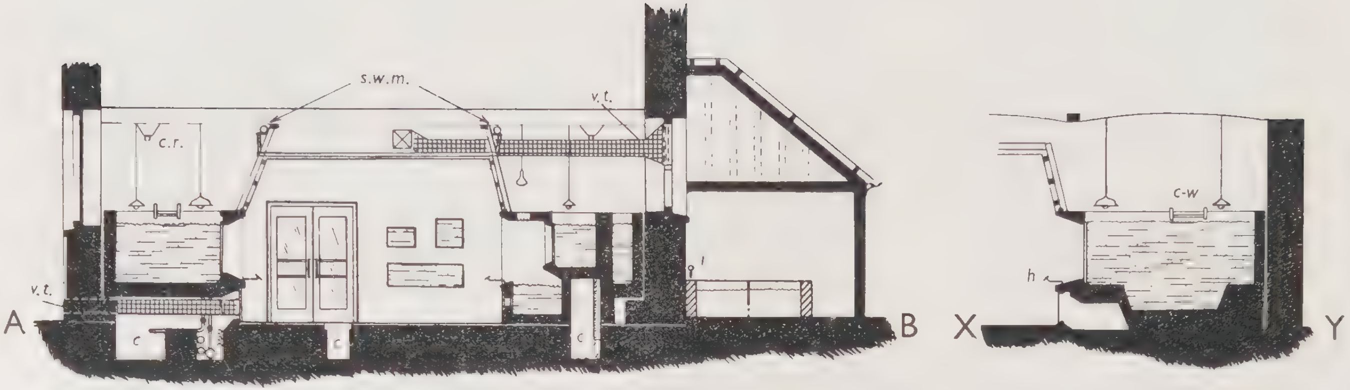


Fig. 2

Text-figs. 1 and 2. Plan and sections of the new aquarium and new outside circulation. Water in the exhibition tanks is indicated by line and dot stippling. *c*, sea-water return culvert; *c.b.*, circulation bench; *c.r.*, overhead conveyor rail (Henderson track); *c-w*, cat-walk; *h*, hand-rail; *i*, inflows; *o*, overflows; *p.b.*, plunger bucket; *s*, sill; *s-w*, swim-ways; *s.w.m.*, sea-water main.

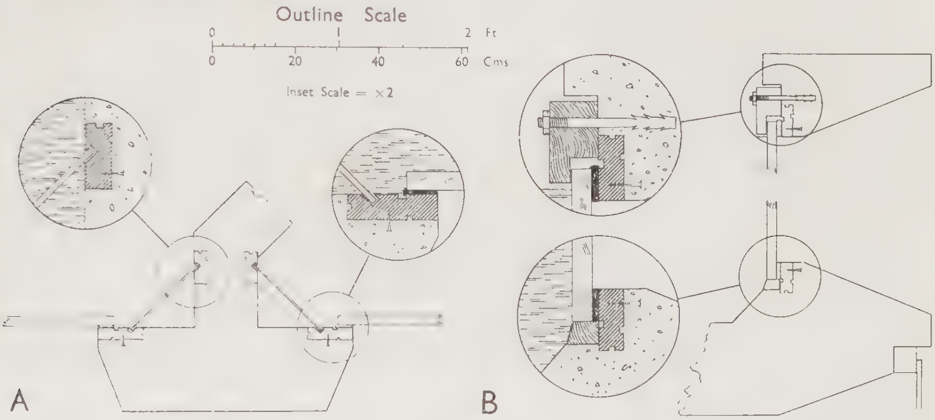
in the sill, about 3 ft. above floor level and nearly 2 ft from the glass, gives some protection to the latter and to the label frames and is a comfortable support to lean on whilst watching the fish.

The hall is ventilated by an extraction fan discharging to the outside at the north-west corner (Text-figs. 1, 2). Trunking above the suspended ceiling draws air through three louvred openings flush with the acoustic tiling. Air enters the hall through trunking passing under the tanks from the outside of the building to louvred openings below the sills. There are three such trunks on each side, but one on the south side discharges into the emergency exit passage, and then through louvres on the inner doors into the public hall. Louvres on the south side can be closed in stormy weather and storm covers are fitted on the outside openings for the winter months. During exceptionally hot calm weather when the aquarium has been crowded it has been necessary to augment normal ventilation by forcing air in through one of the intake trunks on the north side.

Basic construction of the tanks

The new tanks are constructed of reinforced concrete of aluminous cement mixed with local sands and aggregates. Internal surfaces of the back walls and parts of the side walls were subsequently rendered with a waterproof cement and sand mix to seal off hair-cracks. It would be out of place here to give full engineering specifications of the reinforcement and methods of construction; it is feasible to give only an outline description of the tanks as they can be observed in a completed state.

The arrangement and shapes of the tanks will be most readily understood by a study of the plan and sections in Text-figs. 1, 2 and 4. It is instructive to compare these figures with the plan and section of the old aquarium (Wilson, 1952, text-figs. 1, 2). As before, the tanks roof over culverts returning overflow water to the reservoirs; they rest behind on ledges at the bases of the main walls of the building and in front are continuous with concrete pillars extending each stile and window mullion to bedrock below floor level. The culverts are the old ones modified in width and re-asphalted. The old central culvert has been retained for possible future use. The old drainage trenches have been filled in and on the south side a new trench to carry services to the laboratories at the east end of the building has been excavated alongside the southern culvert and under the forward parts of the tanks. These services pass under the big tank. Easy access is provided to all culverts and to the service pipes everywhere. The larger tanks on the north and south sides are 6 ft. wide (front to back) and 4 ft. deep with a water depth of 3 ft. 6 in. Their walls are 6–7 in. thick, their bottoms 8–9 in. thick. Creosoted soft-boards used when casting the back walls of the tanks, to prevent the concrete adhering to the walls of the building, remain in position. The big tank at the east end is internally 29 ft. long and varies in width from about 8 ft. 4 in. at the centre to about 9 ft. 3 in. near each end. The bottom of this tank is about 10 in. thick, and at the north end it drops down to a lower level over an area irregular in shape, thereby increasing the water depth at this place by about 1 ft. 3 in. The small tanks with a water depth of rather less than 2 ft. 6 in. occupy the corners between the ends of the big tank and the north- and south-side series. On the north side at the west end a shallow triangular tank overlaps a floor tank which is divisible into two with a removable partition or, as at present, by built-in rockwork. The floor tank is viewed only through the water surface and is designed for the display of flatfishes on contrasted bottom shingles. Except for this floor tank the water surface in all the tanks is at a uniform height, permitting openings to be made between tanks as described below (p. 402).



Text-fig. 3. A. Plan of a stile between a triangular tank on the right and a larger tank on the left, including a portion of the dividing wall with polythene sheets slid into slate slots to form inflow ducts. Inset are details of slotted slate inserts keyed to the concrete by grooving and rustless-steel screws. In the right inset is shown the edge of a glass pane with sealing compound ('Glasticon', drawn solid black) between it and the slate.

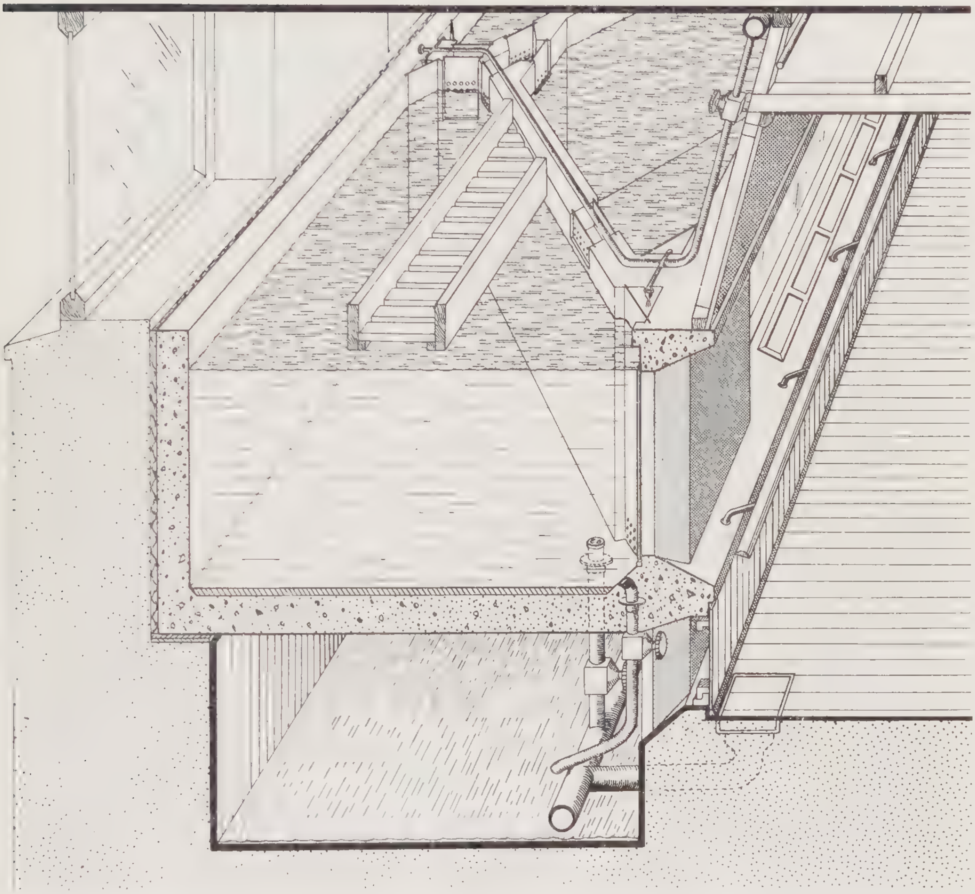
B. Section of a tank front showing lintel walk-way and sill. Inset above are details of teak turnbuckle on rustless-steel rag-bolt, top edge of glass, water level, etc. Inset below shows bottom edge of glass resting on teak block on ledge of sill with details of grooved slate inserts, sealing compound, etc.

Except for the shallower tanks all the window openings are of uniform size, 5 ft. 7½ in. long by 3 ft. high. One advantage of this uniformity is that a single spare pane of glass fits all tanks except the shallow ones. The glass panes, 1 in. thick, overlap the window opening 1½ in. all round. These openings are formed of slate inserts keyed to the concrete (Text-fig. 3). The slates are grooved to give facings exactly 1½ in. wide. This is necessary to achieve uniformity of pressure on the sealing compound and to aid in positioning the glass. The glass is pressed by water pressure against the sealing compound 'Glasticon' ('Glasticord' 304) laid in strip form on the facings (for method of glazing see Wilson, 1952, p. 195). A single teak turnbuckle fixed to the frame above the middle top edge of each pane prevents accidental falling inwards of the glass when the tank is emptied.

The top edges of all window openings are 5 ft. 7 in. above floor level all round the aquarium. The heads or lintels are wide and flat topped, they carry the sloping sides of the suspended ceiling and form convenient walk-ways for servicing the tanks (Pl. II, fig. 1), especially for glass-cleaning. The sills are also wide and carry externally the label frames and support the hand-rail already described. Within each tank the sill provides a ledge 1½ in. wide on which the bottom edge of the glass pane rests, though indirectly with two teak blocks near either end between it and the concrete (Text-fig. 3). From this ledge the sill slopes downwards at 45° to the tank floor (Text-fig. 4). This slope, about 4 in. wide, cannot be seen by the public; it ensures that sand is kept well away from the glass and the glass-cleaning brush. At one place in this slope a 2 in. diameter drain hole, guarded by a plug, leads through a polythene pipe (with puddle-flange) to a Saunders-type valve under the sill to allow, after removal of the plug, the tanks to be drained into the culvert. A similar drain hole, plug and valve is situated close by on the tank floor; through this valve the tank can be drained to waste, a convenience when the emptied tank is cleaned by hosing. To prevent unsightliness the floor plug is normally covered over with sand or gravel: the plug in the sill is, by virtue of its position, out of sight. Below the front edge of the sill fluted asbestos sheeting with removable panels conceal the drainage valves and the culvert. A number of covered floor drains in the public hall are provided for washing down the floor.

Circulation

At the time of writing the same two centrifugal pumps mentioned in a previous paper (Wilson, 1952, p. 204) maintain the circulation, but new pumps of larger capacity will be installed in the near future. The old 4 in. vulcanite main rising from the engine room in the north-west corner (Text-fig. 1) feeds into a new 3 in. black polythene ('Alkathene') pipe which divides into two branches, each controlled by a Saunders valve, one to the north-side tanks and one to the south. These two mains run close to the true ceiling above the corner of the suspended ceiling (Text-figs. 2, 4); there they are readily accessible. Cleaning eyes are provided at bends where needed. From these high-level mains down-dropping 1½ in. pipes, also of black polythene and controlled by Saunders valves, lead through smaller branches to nozzles injecting water into the tanks (Text-figs. 4, 5 and Pl. II, fig. 1). In the old aquarium the mains lay along the tops of the tanks not far above water level and numerous nozzles injected water and air bubbles into the tanks. Not only were these mains an obstruction to servicing but the inflow method was inefficient, for only a portion of the water ever reached tank bottom and



Text-fig. 4. Section through a north-side tank incorporating perspective view facing east and showing portions of three tanks and part of the public hall. Behind the tank is the main wall of the building with a window. The back of the tank rests on a footing of the wall, but indirectly on copper plates forming a sliding bearing to allow for possible movement; the plates are sealed from the sea-water circulation. Between the back wall of the tank and the wall of the building is a layer of creosoted soft-board which during construction prevented the liquid concrete from adhering to the building. Under the tank is an asphalt-lined sea-water return culvert within which is a drain pipe running to waste From this drain pipe there is a connexion, through a valve, to the tank floor and through an open pipe another branch leads to a covered sump in the public hall. A drain in the tank sill, controlled by a valve, can discharge water into the culvert and so back to the reservoirs. At the apex of the triangular tank there is an overflow serving all three tanks, a swim-way between the two larger tanks, and to the latter an inflow each. These structures are shown in greater detail, viewed from above, in Text-fig. 5. A portion of a cat-walk is shown, and in the wall on the nearside a safety overflow from the triangular tank is seen. Still farther forward are two inflows, one of them to the triangular tank. The polythene branch pipe, with Saunders valve, serving the inflows, leads down from the sea-water main at ceiling level. Nearby is the main compressed-air pipe, but no valves or branch connexions to this are shown. In the public hall are seen the hand-rail with supports inserted in the concrete sill; label frames between it and the glass; and below the sill, fluted asbestos sheeting down to floor level.

much of it quickly disappeared down the overflows (Wilson, 1952, p. 199). In the new aquarium all the inflowing water enters at or near the bottom. The nozzles spray the water into corners of the tanks cut off by sliding sheets of black polythene perforated near their bottom edges with rows of small holes (Text-figs. 4, 5 and Pl. II, fig. 1), or spray it into special channels inset in side walls, or into large-bore pipes with similar rows of holes at their lower ends. In the large tank these pipes are concealed behind the window mullions. In this way the incoming water is aerated and led directly to the bottom. The depressed area in the big tank is provided with a special inflow pipe functioning in much the same way. None of these inflows is visible from the public hall. During the long and warm summer of 1959 when aquarium temperatures were unusually high (over 18° C for 6 weeks) almost all the animals were in better health than had been usual with the old aquarium even for a normal summer.

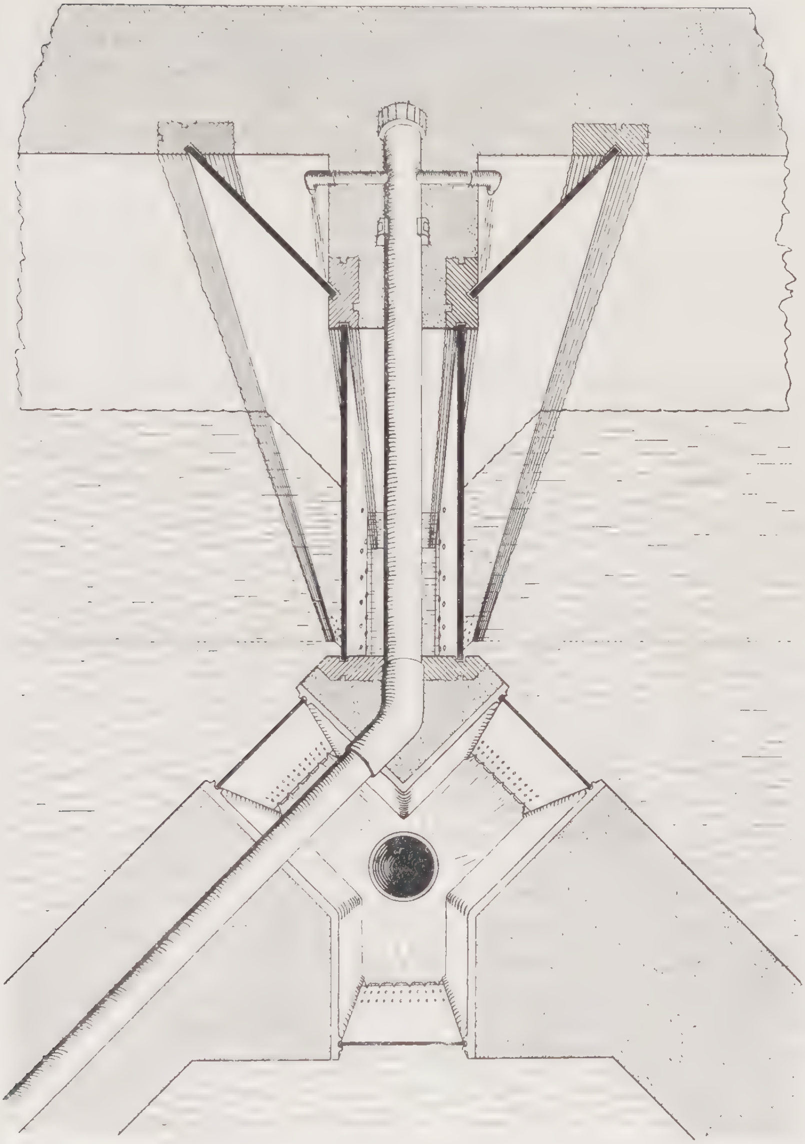
Asbestos overflow pipes of 4 in. bore are cast into the concrete walls, mainly at the apices of the triangular tanks. A view looking down on one of these is seen in Text-fig. 5. Short asphalt-lined passageways lead the overflow water from three tanks to the overflow pipe, which discharges it directly into the underlying culvert. The entrance to each passage is guarded by a perforated sheet of polythene held in grooves formed in asphalt. The V-shaped notches in the lower edges of these sheets ensure that the surface-film water is drawn off; this is important, for should the surface-film be trapped a scum of dust from the air and oily matter from food, etc., will accumulate over the whole surface. Through the side walls of each triangular tank openings slightly above normal water level are fitted with perforated vulcanite sheets held in slate grooves (Text-fig. 4 and Pl. II, fig. 1); these are safety outlets should the proper overflow become obstructed. On the south side there are three overflow pipes serving six tanks; four overflow pipes serve four north-side tanks, the big end tank and the two corner tanks, and all seven tanks can overflow into one another. It is thus impossible for tanks to overfill unless all overflow pipes of a series are simultaneously blocked, which is virtually impossible.

The divisible floor-tank in the north-west corner has two large-bore overflow pipes draining away surface-film water to keep it clear.

Compressed air

In the new aquarium compressed air is used for two purposes only: (1) for lifting water from lower levels to the surface, thereby assisting in maintaining water movement within the tanks; (2) for imparting a rippled surface to bring about a play of light and shade over rocks and gravel, as occurs naturally in shallower regions of the sea.

The air is bubbled up inside pipes of 3 in. bore (concealed behind two window mullions on the north side), or in tank corners behind polythene sheets



Text-fig. 5. Perspective drawing looking down on an overflow serving three tanks, a swimway between two tanks, and inflows to two tanks. The top faces of the concrete are stippled; of the slate inserts hachured; while the top edges of the sliding polythene sheets are solid black. The top edges of the asphalt lining of the overflow channels are unshaded. Water is shown by dashed lines.

(Pl. II, fig. 1). Water is drawn in through holes near the bottom of the pipes or sheets and gushes out through slits slightly above water level. Experience and experiment in the old aquarium showed that such 'air-pipe pumps' use compressed air much more effectively than diffusers sited openly on tank floors.

Facilities for servicing

The walk-way on the lintel, used mainly when brushing the inside surfaces of the glass panes, has already been mentioned. Slatted ash-wood cat-walks, 18 in. wide on north and south sides (Pl. II, fig. 1), 2 ft. wide over the big tank at the east end, rest on the tank walls or on concrete tie beams. (There are two tie-beams on the north side and two across the big east tank; they connect, above water level, the mullions to the back walls of the tanks, but are not shown in any of the figures illustrating this paper.) The walk-ways and cat-walks make it easy to move round the whole of the aquarium above the tanks, at one point passing over the roof of the emergency exit. They greatly simplify all servicing operations, making the work less time-consuming and laborious than in the old aquarium.

Attached to the ceiling along most of the north side and the whole of the south, lengths of overhead track (Pl. II, fig. 1) provide convenient hand-rails above one edge of the cat-walks and serve for the easy transport of heavy objects.

For cleaning purposes a small electric 'Mono' pump has been provided. With flexible hoses and various shaped suction nozzles it is possible to suck out silt from gravel floors, off the rocks, etc. A coarse filter, or sieve-box, has been fitted on the suction side of the pump to protect it from damage when gravel is accidentally sucked up. The discharge is passed into the nearest convenient overflow pipe. With the reservoir sedimentation system now in use (see below) it is no longer necessary to run muddy sea water to waste when cleaning, necessitating subsequent pumping up from the sea to make good the loss.

A special servicing feature are the 'swim-ways' in the walls between the larger tanks (see especially Text-figs. 4, 5). These openings (approximately 1 ft. wide, extending below the water level for about a foot) are normally closed each by two sheets of black polythene slid into grooves; the sheets are perforated above water level to allow of their functioning as additional safety overflows. These openings, once the sheets are removed, permit fish to be swum from one tank to another as desired. Thus during a major tank-cleaning operation the fish of one tank will be netted and removed to storage tanks in the yard, choosing for netting easily caught and not readily damaged species such as dogfishes and conger eels. The swim-way adjacent having been made watertight (with a bolted-on cover and sealing compound) this tank will be emptied, cleaned and reflooded. The swim-way will then be opened and the fish in the next tank (species such as whiting which are easily damaged by netting) will be driven through into the cleaned tank and shut off there. Their tank in its turn will be emptied and cleaned and made ready for the reception of fish from a tank farther on. Finally, when the whole series has been emptied and cleaned one at a time, the fish will be driven back into their own tanks and the dogfishes and conger eels brought back from the yard. In this way handling of fish will be reduced to a minimum.

In the north-west service area (Text-fig. 1) a number of small asbestos tanks are used to store live food (shrimps, crabs, mysids, worms, etc.) and to accommodate recently caught small animals until such time as they are placed in the exhibition tanks. This corner also houses the 'plunger-bucket' (to work 'plunger-jars' in a laboratory above) which is supplied with water from the north-side series of tanks.

Lighting

It is hardly possible to light an aquarium satisfactorily by daylight. Daylight is too variable in intensity and whatever the orientation of the tanks some will always be more brightly lit than others. When the sun shines strong reflexions of the sunny side will be seen in the darker side unless a curtain, as in the old aquarium, be hung down the middle of the public hall. Too much daylight induces rapid growth of small algae which on dying break up and produce silt; the result is dirty tanks. Back-lighting from windows behind the tanks, a standard feature of many Victorian public aquaria some of which still survive, illuminates the sides of the fish away from the viewer and leaves the backs of the tanks in semi-darkness. A few translucent objects—some sea anemones, ascidians, dogfish eggs, etc.—look well when back-lit but the majority of opaque animals do not. The tanks should be more strongly lit than the public hall, to avoid as far as possible reflexions of people in the glass and to make the tanks appear as a series of bright living pictures within their darker frames.

To exclude daylight the south-side windows have been fitted inside with asbestos sheeting. On the side facing the glass the sheeting is enamelled dark blue, purely as an architectural feature when seen from outside the building. Three windows have been left to open to obtain ventilation while admitting a minimum of daylight (Pl. II, fig. 1). On the north side the windows are sufficiently screened from the sky by the roof over the new outside tanks (see below).

The public hall (Pl. I) is lit mainly by light passing through the tanks aided by a series of recessed lights in the suspended ceiling. It is dim but not completely dark, there being sufficient illumination to see any object on the floor and to allow the Guide Book to be read.

Over the tanks two lines of electric conduit tubing are fixed at main ceiling level, one between the cat-walk and the glass and the other between the cat-walk and the backs of the tanks (Pl. II, fig. 1). At selected points screwed waterproof three-pin sockets are provided from which hang the lights, the heavier ones on chains. Over most tanks there is one main light (usually a 200 W., occasionally 100 W. bulb inside a watertight reflector fitting) 12 in. above water level and 12 in. from the top edge of each glass pane. The back lights are more numerous and more variable; they are mostly 100 W. bulbs in watertight fittings, but fluorescent tubes, protected from damp, are used in places. The back lighting has been arranged to give the most effective illumination of the rock scenery and therefore varies from tank to tank; the front lighting is more constant as it is intended mainly to illuminate the animals. The triangular tanks have only one light, the front one, but special effects can be arranged if needed. Front and back lights are independently fused and switched.

In addition to the main lights, low-wattage bulbs in waterproof plastic bulkhead fittings fixed at a small number of places on the ceiling directly above the tanks (Pl. II, figs. 1) are switched on whenever the main lights are off. These night-lights give sufficient illumination for a number of active fishes to avoid obstructions at night. They probably help the mackerel and some other pelagic fish and they definitely do help Smooth Hounds (*Mustelus mustelus*) and Spur Dogs (*Squalus acanthias*) to avoid bumping their snouts on rocks in the dark. The provision of night-lights was recommended long ago by Saville Kent as a result of his experiences in the former Manchester Aquarium (opened 1874) and their benefit to these same species was noticed independently at Plymouth some years ago.

The floor-tank is lit partly from above by flood-lamps shining down through holes in the canopy over the tank, and partly from lamps behind plate-glass windows in the front wall below water level. The lights are so masked and positioned that they illuminate only the floor of the tank, and none of the surrounds above water level. No lamps or their reflections are visible from normal viewing positions.

At suitable points on the walls behind the tanks three-point 5-amp switch sockets are provided. These are intended for the electric cleaning pump but are available for special or temporary lighting if required.

Rockwork

Few fish are completely at ease in a bare-walled tank. Many invertebrates and some fishes need to be provided with rocky nooks and crannies and with a floor of natural sands or gravels. When an aquarium is intended to attract a paying public the appearance of this rockwork and the treatment of the tank walls is of paramount importance in providing an aesthetically pleasing background against which the animals are viewed. The success or otherwise of the scenic presentation cannot fail to influence receipts at the cash desk.

As the Plymouth aquarium is intended almost entirely for local marine life it was decided to base the scenic presentation on local rocks and of these the beautiful Devonian limestone forming the northern boundary of the Sound was considered most suitable. The rock is very hard and is often bluish white in colour, pink or streaked with pink. Water-worn rocks of various sizes could be picked up from higher tidal levels, and by careful attention to bedding planes could be built into natural-looking cliffs in the tanks. In addition to the use of real rocks rubber-latex moulds were made of small portions of water-worn cliff faces and used to produce artificial rock 'tiles'. One face of each tile exactly reproduces the shape and texture of the natural rock on which the mould was made. The other face, being flat and scored, forms a 'key' for cementing to the back walls, especially of the triangular tanks where it is necessary to keep the thickness of the added rockwork to a minimum. Joints between adjacent rock tiles are filled with cement and sand and modelled to merge the natural mouldings of the various tiles into one apparent solid rock face. A little of the rockwork in one triangular tank is seen in Pl. II, fig. 1. A strong mix (1:3) of sulphate-resisting cement and crushed limestone which had passed a ¼ in. sieve was used in making the tiles. Before filling the moulds with the mix the rubber was wetted with a strong solution of 'Teepol' to prevent the adhesion of air bubbles and, after filling, the moulds were vibrated to eliminate all air trapped in the mix. For fixing the tiles to the tank walls a stronger mix (1:2) of sulphate-resisting cement, fine sands and waterproofer was used. Finally, the artificial rock faces were painted to resemble natural rocks. The epoxy resin paints used are non-toxic, are very hard and should withstand repeated cleaning. The final effect is excellent, it being difficult to distinguish artificial rocks from natural and impossible once they are covered with natural growths.

Where the back wall of a tank is left bare it is painted with epoxy resin paint of a moderately dark-green shade to simulate the effect of the greenness seen on looking through many feet of sea water. Near the backs of certain tanks frosted (sand-papered) sheets of Perspex pleasantly diffuse the background to give an appearance of distance; they eliminate shadows which would otherwise show on the walls. Scenic paintings of apparently distant rocks on the walls behind such sheets increases this illusion of remote vistas. The sheets are mostly 6 in. in front of the back wall of the tank, but sometimes are farther away and fish allowed to pass behind. They are held by slotted slates hidden in the rockwork. In arranging such sheets it is essential that side and bottom edges be concealed from view, for if seen the illusion is destroyed.

The angled-out side walls of the larger tanks are painted white (Pl. II, fig. 1), again with epoxy resins. This white surface is, of course, invisible to the public and it helps to reflect back into the tank some light which would otherwise be lost. To conceal the far corners of these tanks, with their inflows and swim-ways, rock cliffs are built against the side walls a little in front of them.

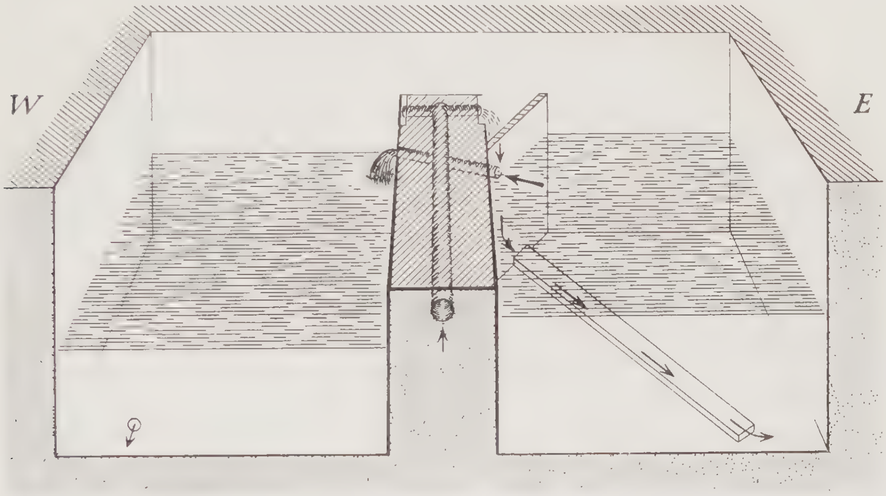
Fish can pass out of sight behind these cliffs but most fishes remain in view. Only lobsters, dogfishes, conger eels and wrasses have been troublesome, often hiding in the concealed corners, and special measures are taken to deal with them. Thus if there are more lobsters in a tank than there are hidden corners some will be forced to occupy holes in full view. Fish swimming into view from behind these cliffs and disappearing again behind them seem to come and go as they would naturally do among rocks in the sea.

After the rockwork was built the bottom of every tank was covered with a layer of sulphate-resisting cement and sand, to which a suitable yellow colouring agent had been added, and rendered to a thickness of an inch. While still wet the rendering was strewn with sand or gravel, gently patted in by hand and given a rippled surface as on a sandy sea shore. Now when fish disturb the loose sand or gravel the rippling helps to retain it in position and where patches of floors are uncovered they match well the sand or gravel and do not look like bare concrete. It is important that the bottom screeding be carried out after the rockwork is in position so that rocks emerge from it as from a natural deposit.

Aquarium reservoirs and water treatments

The provision of clean well-aerated sea water of as near normal chemical and physical constitution as possible is essential to the well-being of an aquarium. Until very recently the water supplied to the tanks of the Plymouth aquarium (from reservoirs for a description of which see Wilson, 1952, p. 204) has always been loaded with varying quantities of silt, although generally satisfactory in other respects. Quite early in the history of the place much effort was expended to free the water from silt, as well as to improve it in other ways. There is frequent reference to these efforts in early Reports of Council and Director's Reports published in early volumes of the *Journal*. Various filters were devised which seem to have functioned for a time but which cannot have proved satisfactory for long. Conditions at one time were evidently so bad that doubts were expressed concerning the efficiency of closed sea-water circulation systems and a single use of water, at least for the laboratory, advocated (*J. mar. biol. Ass. U.K.*, Vol. 4, pp. 77 and 417; Vol. 5, pp. 98–99).

The first major improvement to the condition of the circulating sea water was made when regular treatment with slaked lime (to remove carbon dioxide and restore the pH) was instituted sometime after 1922 (Atkins, 1931). The silt trouble remained and occasions when it was possible to view with some clarity the backs of the largest tanks through 9 ft. of water were regarded as almost noteworthy. Most of the silt was formed in the tanks by the decay of plant growths, the breaking up of faeces, etc., and it was kept in suspension by the stirring activities of the animals, especially bottom fishes. All but the heavier components were carried away in the overflow water and discharged at the surface into one of the two underground reservoirs. From this reservoir water was being drawn off to the pumps at a point about 3 ft. from the bottom, and with it any silt still in suspension. There was thus a steady build-up of suspended particles and the longer the water had been circulating the cloudier it was. The cloudiness of the water in the reservoirs was such that the bottom at a depth of 11 ft. was rarely visible; often it was not possible to see anything at even half that depth. Allowing each reservoir to rest and sediment alternate weeks was only partially successful in clearing the water (see below). The system has been described and criticized in Wilson, 1952, pp. 204 and 209. A method of sedimenting off the silt there suggested has now in modified form been adopted with excellent results.



Text-fig. 6. Diagram of the sea-water reservoirs (not to scale and with roof omitted) to show method of circulation now in use. The direction of water flow is indicated by the arrows.

The method now in use involved no more than minor modifications to the existing reservoirs. These are shown diagrammatically in Text-fig. 6. Water returns from the aquarium along a 1 ft. diameter pipe in the wall dividing east and west reservoirs. At its northern end there is a T-junction where sluices divert the water to one or other of the reservoirs as required; in the old days it would be the reservoir from which water was being pumped, there being then no communication between reservoirs.

During the construction of new underground reservoirs for the new laboratory circulation (see below) the east reservoir had to remain empty for 6 months and only the west reservoir was in use. During this period the water became so dirty that in the aquarium anything farther from the glass than about 2 ft. disappeared from view in a fog of suspended silt. This gives some measure of the partial success of the old method of alternating reservoirs. While the east reservoir was empty a wall was built across its north-west corner and from the bottom of this wall a culvert of brick sides with removable slate top was constructed across the reservoir floor to near its south-east corner. A 6 in. drain pipe was inserted through the dividing wall at the north end, passing under the larger return pipe from the aquarium. With both reservoirs flooded the return water now discharges into the corner cut off by the wall and passes along the culvert to emerge near the south-east corner at the bottom as shown by the arrows in Text-fig. 6. This brings about a continuous overflow of surface water from the east to the west reservoir from whence it is drawn off to the pump through the old suction pipe in the south wall. However dirty the incoming water (as with silt-laden water from the discharge of the cleaning pump), that which rises up to overflow into the west is always crystal clear. The silt settles out over the floor of the east reservoir where mixed with lime (lime is now put into the east reservoir only) it shows no tendency to blacken or smell and could be left there for years. The water in both reservoirs is so clear that the smallest details are visible on the bottoms of both, and visibility in the aquarium tanks is almost always perfect, showing only slight cloudiness on feeding days (due mainly to defaecation) or when fish stir up the bottom gravel. It has been mentioned that after 6 months continuous use of the west reservoir the water in the aquarium was exceptionally dirty, but only 4 days after putting the new system into operation visibility was better than anyone could remember.

Apart from the deposition of silt the new method gives better aeration. Whereas under the old system the returning water was cascaded once into a reservoir to sink down to the pump intake, this water is now cascaded twice. Moreover, it is surface water in contact with air in a well-ventilated space which is cascaded into the west reservoir. Tests of water from the middle depths of the latter have shown close approximations to 100% oxygen saturation.

Means are provided whereby it is easy to revert to the old system of using one reservoir only. This is occasionally necessary for a day or two while one or other of the reservoirs is emptied and cleaned. The method of refilling from the sea was described in Wilson, 1952, p. 205. Sometimes the west reservoir is only partially emptied and the system freshened with new water from the sea pumped into the east reservoir.

The total quantity of sea water held by the reservoirs is about 110,000 gallons when both are completely full, while the total quantity of water in aquarium and service tanks is roughly 17,000 gallons. At the present time the water is circulated at a rate of about 3000 gallons an hour (for description of the pumps see Wilson, 1952, p. 204). This rate is barely adequate, especially in hot weather, and it is desirable to increase the rate to 4500 gallons per hour or even more.

NEW CIRCULATION

An ever-increasing need for more live-specimen storage accommodation, and for research purposes cleaner water less heavily stocked with animal life, led to a decision to build an entirely new circulation system independent of the main aquarium and its ancillaries. Thus, commencing in October 1955 new reservoirs were excavated in the yard between south and north buildings and a new series of outside tanks were built to replace the smaller series illustrated and described in Wilson, 1952, pp. 202–3. The new system was brought into operation for the first time early in September 1957. The contractors for these new reservoirs and new outside tanks were Messrs A. N. Coles (Contractors) Ltd., Plymouth.

New reservoirs

A large hole was excavated in hard limestone to the east of the aquarium reservoirs. In this hole new reservoirs were constructed in concrete (using sulphate-resisting cement) and lined with a rendering of waterproof concrete coated with bituminous paint. They were roofed over at road level with concrete and tarmacadam. The roofing is designed to take a load of 12 tons. At convenient places manholes give access to the reservoirs below. Each reservoir holds about 16,000 gallons of sea water when full and there is a well-ventilated air-space of about 2 ft. between the underside of the roof and the water surface. The dividing wall between the reservoirs has three wide openings 8 ft. 9 in. above reservoir floor level. Water returning from the tanks cascades into a partitioned-off space in the south-east corner of the east reservoir and is there forced to descend to the bottom where silt is deposited. As this east reservoir fills up it overflows the dividing wall through the openings mentioned and cascades into the west reservoir. The depth of the water as it passes over the flat top of the 12 in.-wide wall is very shallow; thus the whole volume of the water as it circulates is at these places brought into close contact with air. From a position 4 ft. above floor level at the west end of the west reservoir the water is sucked away through a black polythene pipe of 3 in. bore to the pumps. The east reservoir is limed weekly through an inspection cover. Provision is made for working from either reservoir only while the other is emptied and cleaned. Each reservoir is provided with a drain hole and plug at its south-west corner and the floor slopes downwards slightly to the drain hole. The 4 in. drain pipe passes under the floor of the new west reservoir and passes through the south end of the old east reservoir of the aquarium circulation to join the main drain. The depth of water in the new reservoirs varies between 8 and 9 ft. when full. The reservoirs are filled through a 4-in. bore iron pipe and through valves connecting with the pumping system used for filling the aquarium reservoirs (Wilson, 1952, p. 205). Compressed air can be supplied to the west reservoir should it ever be needed.

Electric lights in watertight bulkhead fittings are fixed to the roof of each reservoir and are switched from the pump-room in the basement of the south building.

New outside tanks

Under a new roof a new series of outside tanks was used for the first time in September 1957. They comprise (Text-fig. 1 and Pl. II, fig. 2) three blocks of concrete tanks (painted internally with bituminous paint) and nine large (100 gallon) and four small (20 gallon) asbestos tanks on raised plinths (Text-fig. 1). A double tier of slate shelving, built partly against the main building and partly against a wall at right angles to it, forms a circulation unit for bowls and jars. Four of the concrete tanks are divisible by asbestos sheets sliding in grooves; a fifth is bowl-shaped to accommodate squid and cuttlefishes. The water depth of the smaller concrete tanks is roughly 19 in., while the water depth of the large central tank can be varied at will at 23, 31 and 36 in. by placing rubber bungs in the lower overflow holes. All overflow pipes pass down inside the thickness of the tank walls and are fitted with plastic bowl-shaped sieves ('salad-shakers' from a local store) to prevent the ingress of large objects. These overflows discharge into a culvert below ground level which returns overflow water to the reservoirs. The culvert and the lower ends of all overflow pipes are readily accessible through a series of manholes. Inflow pipes are also within the thickness of the walls and discharge into the tanks close to the bottom.

The asbestos tanks are fitted with black polythene piping for inflows and overflows. They can easily be removed and other tanks of different sizes put in their place.

At the time of writing, all tanks east of the circulation benches are supplied from the new reservoirs, while the benches themselves and the tanks west of them are on the aquarium circulation. It is possible for the largest concrete tank and the three asbestos tanks near its western end to be supplied with water from the aquarium circulation should this ever be necessary.

Electric lights for viewing the outside tanks at night are provided under the roofing. It is intended at some future date to fit shutters which in summer will slide up out of the way under the roof, but which in winter can be pulled down to enclose the tank space and protect the system from frost.

New pumps

The new circulation is maintained by paired 'Mono' pumps with stainless-steel impellers inside rubber stators. Driven by 3 h.p. three-phase motors each unit delivers about 3600 gallons an hour. One pump is run for several weeks while the other is serviced and rests as a stand-by. Adjustments to the gearing of the V-belting will enable these pumps to give a greater output should this in future be needed. At present the output is more than ample as it is serving only the outside tanks and those on the first floor of the main laboratory (as described in Wilson, 1952, p. 203,[1] and illustrated in Russell, 1948, pl. XIX).

Circulation efficiency

The total capacity of the outside tanks and those on the first floor is about 2600 gallons; this being less than a twelfth of the reservoir capacity, a much smaller proportion of tank volume to reservoir volume than in the aquarium circulation. The relative rate of flow of the water is also much greater. Even when eventually more experimental tanks in the new block of buildings now being planned are added the new circulation will contain less animal life per unit volume than the aquarium circulation, and be relatively more efficient in every way except temperature stability. There is no regular means of heating or cooling either circulation, and while temperature changes are slow the new circulation is more affected by the weather than is the old. This is because the total volume of water is less than in the aquarium circulation and a greater proportion of it is exposed to air temperature and wind in the yard. When shutters are fitted to close in the outside tanks in winter it will be possible to reduce the rate of loss of heat, though it is doubtful if shutters will help to check rise of water temperature during hot days in summer.

My thanks are due to Mr G. A. W. Battin for making the drawings for this paper and Mr A. C. G. Best for help with the photography.

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[1] Except that the overflow water from these main laboratory tanks no longer runs into exhibition tanks in the aquarium below but is conducted by new piping to the return culvert to the new reservoirs.

EXPLANATION OF PLATES

Plate I

General view of the new aquarium from the public entrance lobby. Note the handrail, label frames, ceiling with inset lights, etc. (A photograph of the old aquarium from almost the same viewpoint is reproduced in Russell, 1948, pl. XXIII, fig. 1.)

Plate II

Fig. 1. View along the tops of the tanks of the south side from the west end. Note especially the shapes of the tanks, the lintel walk-way and cat-walks, the overhead conveyor track, details of inflows and overflows so far as visible, sea-water and compressed-air pipes (one of the latter on tank-back near right foreground), light fittings, etc. Compare especially with Text-figs. 4 and 5.

Fig. 2. View of new outside circulation tanks and circulation bench from the western end. Note in right foreground a pair of concrete tanks painted internally with black bitumen. Further on is the double-tiered circulation bench for bowls, and, in front, four small asbestos tanks on a low circulation table. Behind the circulation bench the outer of three large asbestos tanks, on a raised plinth, is seen. Farther on still is the large and deep concrete tank, then a pair of shallower concrete tanks similar to those in the foreground. Beyond these part of a row of three large asbestos tanks is just visible. (For photographs of the old outside circulation which these tanks replace see Russell, 1948, pl. XXII, fig. 2, and Wilson, 1952, text-fig. 4).

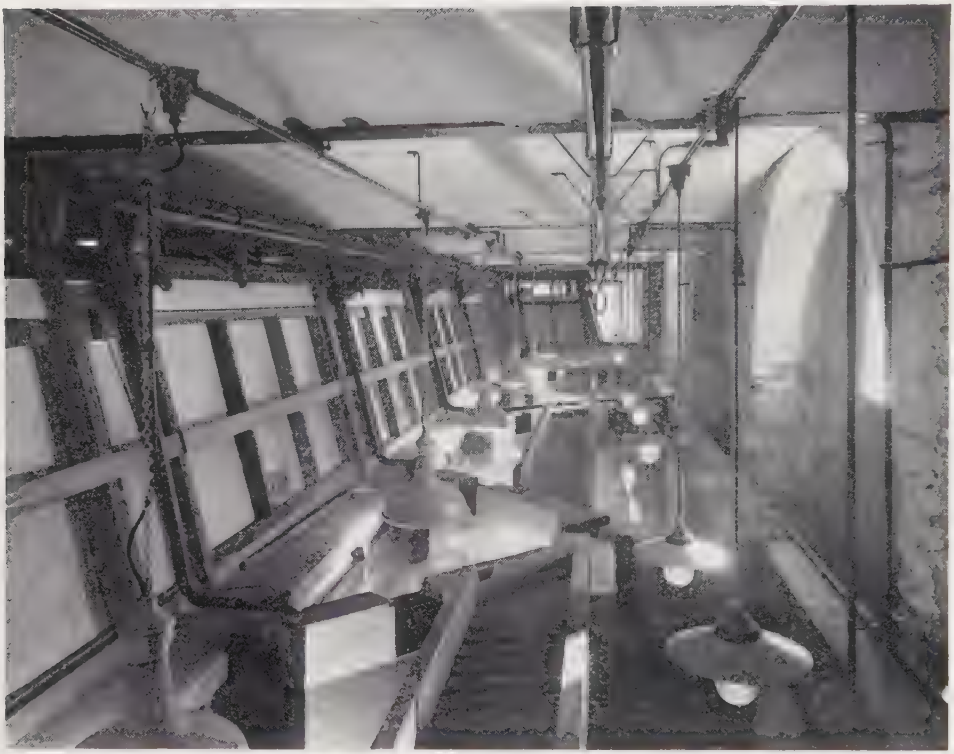


Fig 1

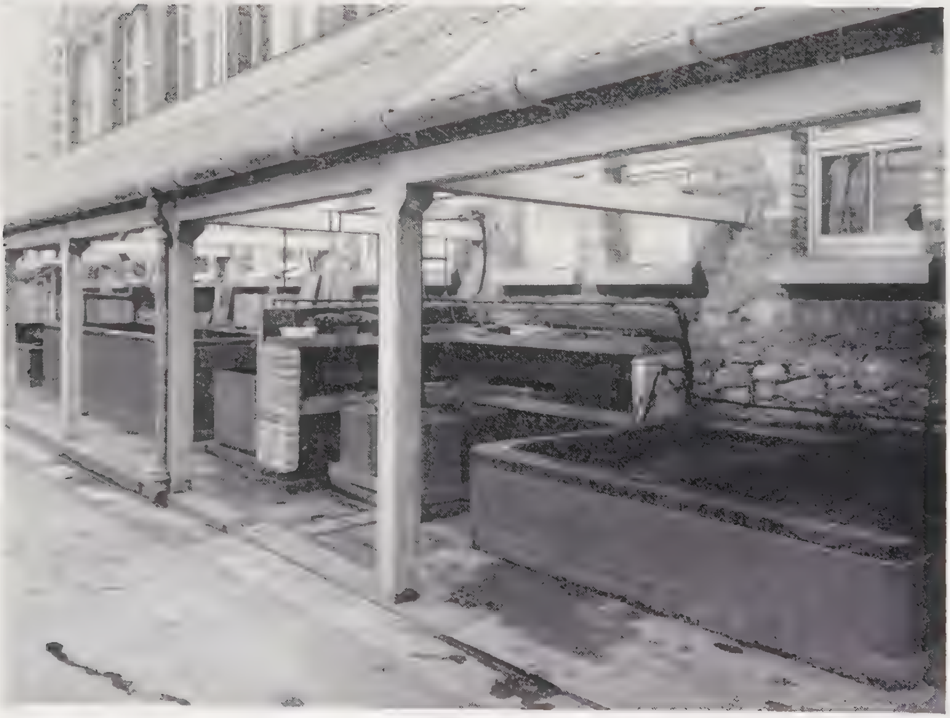


Fig. 2.

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Boney, A. D., Corner, E. D. S. & Sparrow, B. W. P., 1959. The effects of various poisons on the growth and viability of sporelings of the red alga *Plumaria elegans* (Bonnem.) Schm. *Biochem. Pharmacol.*, Vol. 2, pp. 37–49.

Mercury, silver, copper and arsenic are more toxic than the non-metallic inhibitors hydrocyanic, hydrazoic, iodoacetic, fluoroacetic and malonic acids and 2:4-dinitrophenol to sporelings of *Plumaria elegans* in sea water at pH 8·1. Mercury and silver are more toxic than copper and arsenic, and the toxicities of mercury and arsenic are greatly increased when these poisons are used as lipophilic organic compounds (e.g. phenylmercuric chloride and phenarsazine chloride). All heavy metals are less toxic when used in the presence of reduced glutathione.

The toxicities of an homologous series of primary *n*-alkyl-mercuric chlorides increase to a maximum with that of n-$C_5H_{11}HgCl$. Lipoid solubilities based on methyl-oleate: sea-water partition coefficients correlate with appropriate toxicity data for the first three members of the series, but those of n-C_4H_9HgCl and n-$C_5H_{11}HgCl$ increase without any corresponding rise in toxicity. The 'cut-off' in relative toxicities within the homologous series is not found in complementary experiments with crustaceans.

Mercuric iodide is much more toxic than $HgCl_2$ to *Plumaria* and crustaceans, but whereas various organic compounds of mercury become markedly more toxic to crustaceans when used in the presence of excess KI, their toxicities to *Plumaria* are not increased.

E.D.S.C.

Bursa, A. S., 1959. The genus *Prorocentrum* Ehrenberg. Morphodynamics, Protoplasmatic Structures and Taxonomy. *Canad. J. Bot.*, Vol. 37, pp. 1–31.

The morphodynamics of *Prorocentrum* have been studied comparatively in cultures and in plankton. Plankton populations show little morphological variation. In cultures a variety of forms, often similar to other species of *Prorocentrum* which have been described from distant seas, are found. Morphological variation in *Prorocentrum* species depends upon various life phases, individual features of the clones, and various types of cysts. Formation of the morphological aberrants is also affected by ageing of cultures. All protoplasmatic structures, including the cell membrane, possess their own particular features, changing in course of life cycle. Since both physiological and morphodynamic metabolisms are inseparable in their activities, it is useful to complete taxonomic diagnoses with physiological observations. Five new species are described: *Prorocentrum cordiformis*, *P. pomoideum*, *P. pyrenoideum*, *P. redfieldi* and *P. levantinoides*. Morphodynamics in *P. micans* and *P. scutellum* was also studied. Most observations were made *in vivo*. Specific morphological differences in form and structure of protoplasmatic organelles were demonstrated in each species concerned. An attempt was made also to base taxonomic diagnoses upon the apical tooth, trichocysts, and membrane structure.

A.S.B.

Carlisle, David B., 1959. On the neurosecretory system of the brain and associated structures in *Sipunculus nudus*, with a note on the cuticle. *Gunma J. med. Sci., Maebashi*, Vol. 8, pp. 183–94.

In *Sipunculus nudus* a pair of dorsally situated postero-lateral groups of neurosecretory cells in the brain contain each about thirty large cells. The axons run forward to the unpaired sensory organ, a cavity in the brain connected to the mouth region by a ciliated canal. Here the axons make abrupt loops among the sensory cells of this organ and then run into the finger organs, where they terminate in typical neurohaemal endings, vertical to the blood space surrounding the organs. These club-shaped endings are filled with a secretion which has staining properties different from those of the material found more proximally in the axons and cells. The likeness of this system to the hypothalamo-hypophysial system of vertebrates and to the major endocrine systems of crustaceans and insects is emphasized.

The cuticle consists of protein with no trace of chitin or mucopolysaccharides.

D.B.C.

Carlisle, D. B. & Ellis, Peggy E. 1959. La persistance des glandes ventrales céphaliques chez les Criquets solitaires. *C.R. Acad. Sci., Paris*, T. 249, pp. 1059–60.

The ventral glands of locusts, which are homologous to the prothoracic glands of Lepidoptera and probably to the Y-organs of crustacea, normally disappear in the adult insect. In locusts in the solitary phase, however, they may persist in a functional condition.

D.B.C.

Cooper, L. H. N., 1957. Some chemical and physical factors controlling the biological productivity of temperate and tropical oceanic waters. *Proc. 8th Pac. Sci. Cong.* 1953, Vol. III A (received by the author 1959).

Differences in conditions of productivity in tropical and temperate latitudes were discussed. A pattern for observation and experiment in tropical seas was proposed. Much of the material in the paper has now only historic interest.

L.H.N.C.

Corner, E. D. S., 1959. The poisoning of *Maia squinado* (Herbst) by certain compounds of mercury. *Biochem. Pharmacol.*, Vol. 2, pp. 121–32

When *Maia* is immersed in sea water containing added $HgCl_2$ the concentration of the poison in the blood eventually rises above that in the external medium; the concentration in the antennary glands above that in the blood; and the animals excrete small but increasing amounts of mercury in the urine. Most of the poison present in the blood is attached to protein and the concentration of mercury in the blood remains constant for several weeks after poisoned animals are returned to the sea. Mercury also concentrates in various other body tissues, and very large amounts are found on the gills. Similar results are obtained when the poison is administered to the animals by injection. When, however, the poison used is $n\text{-}C_5H_{11}HgCl$, although mercury again concentrates at the gills and in various internal organs, the amount detected in the blood is very small and none is found in the urine.

When the animals are immersed for progressively longer times in sea water containing added $HgCl_2$, or are injected with increasing amounts of the poison, the total quantity of amino-N in the urine increases, although that in the blood remains constant. The urine : blood ratio of amino-N also rises when the animals are poisoned with $n\text{-}C_5H_{11}HgCl$

although, in this case, the level of amino N in the blood rises as well as that in the urine. Animals poisoned with $HgCl_2$ and then returned to the sea show an abnormally high urine: blood ratio of amino-N several weeks later. By contrast, poisoning with $HgCl_2$ has no effect on the urine:blood ratio of total sulphate. E.D.S.C.

LOWENSTEIN, O. & WERSÄLL, J., 1959. A functional interpretation of the electron-microscopic structure of the sensory hairs in the cristae of the elasmobranch *Raja clavata* in terms of directional sensitivity. *Nature, Lond.*, Vol. 184, pp. 1807–8.

An electronmicroscopic study of the sensory epithelia in the ampullae of the semicircular canals of the labyrinth of *Raja clavata* showed that the hair processes of the sensory cells are compound structures consisting of a number of protoplasmatic filaments, one of which has the typical electron-microscopic structure of the kinocilium, namely nine peripheral plus two central longitudinal fibrillae. This kinocilium is always found on one and the same side of the hair process in a given sensory epithelium and is placed on that side of the sensory hair process which faces in the direction in which the hair process is deflected on excitatory cupula displacement. It appears that this arrangement may be of fundamental functional significance. O.L.

POTTS, W. T. W., 1959. The sodium fluxes in the muscle fibres of a marine and a freshwater lamellibranch. *J. exp. Biol.*, Vol. 26, pp. 676–89.

The efflux of ^{24}Na from the isolated ventricles of *Mytilus* and *Anodonta* has been measured at 15° C and at 5° C. The efflux of sodium in each case is divisible into an extracellular and an intracellular portion except at 15° C in *Anodonta* where the two portions are not clearly distinguishable. The mean rate constant for the efflux of sodium from *Mytilus* ventricle is 2·44 h^{-1} at 5° C and 5·6 h^{-1} at 15° C. The mean rate constant for *Anodonta* ventricle at 5° C is 4·6 h^{-1}. The efflux of sodium from the muscle fibres of *Mytilus* ventricle averages 12×10^{-6} mM/cm^2/sec at 5° C and 27×10^{-6} mM/cm^2/sec at 15° C. For *Anodonta* at 5° C it averages $3{\cdot}1 \times 10^{-6}$ mM/cm^2/sec. If the efflux is maintained entirely by an active process then the energy required for the extrusion is 0·26 cal/g/h at 5° C and 0·63 cal/g/h at 15° C for *Mytilus* muscle and 0·046 cal/g/h at 5° C by *Anodonta*. W.T.W.P.

WICKSTEAD, J., 1960. A new record of *Mytilicola intestinalis* Steuer, a parasitic copepod of mussels. *Nature, Lond.*, Vol. 185, p. 258.

Two mature female *Mytilicola intestinalis* Steuer, 7·0 and 8·5 mm long, were recorded from a locality much removed from the limits of their accepted distribution. They were taken free in the plankton in the northern Malacca Strait area, 7° 12′ N., 97° 12′ E. After various considerations, no satisfactory explanation could be given for their capture at such a place in such a manner. J.W.

WICKSTEAD, J. H. & BONE, Q., 1959. Ecology of acraniate larvae. *Nature, Lond.*, Vol. 184, pp. 1849–51.

Several species of acraniate larvae were obtained during a survey of the Indo-Malayan plankton made by the Singapore Regional Fisheries Research Station. Larvae of *Branchiostoma belcheri* Gray were found at a permanent station in the Singapore Strait from mid-October to January. They showed diurnal vertical migratory movements, remaining on the sea-bottom during the day, and rising to the surface at dusk.

Examination of the gut-contents showed that feeding probably only takes place at the bottom. It is suggested that light intensity is the actuating stimulus for the migration (salinity and temperature variations being insignificant), and that it serves both to distribute the species and to enable the larvae to avoid the attacks of nocturnal bottom-feeding predators.

Larvae of *Branchiostoma malayana* Webb, and larvae of the 'amphioxides' type (but belonging to the Branchiostomidae) were obtained at another station, on the surface, at night. This station was over deep water, and examination of the gut contents showed that the larvae fed in mid-water, hence these species are probably truly pelagic, and never live near the bottom. At a third station, 'amphioxides' larvae of *Asymmetron lucayanum* Andrews were collected, which confirms the identification of *Amphioxides pelagicus* Gunther as the larva of *Asymmetron lucayanum*. Q.B.

BOOK REVIEW

DIE WESTKÜSTE SÜDAMERIKAS IM BEREICH DES PERU-STROMS

BY E. SCHWEIGGER

Heidelberg-München: Keysersche Verlagsbuchhandlung GmbH, 1959.

This comprehensive work has been written by a German who has spent thirty years studying the Peru current and its manifold influence on the neighbouring land, sea and air. Its greatest value may be as a critical digest of an enormous literature about the west coast, published in periodicals with limited circulation and mostly in Spanish. The task the author set himself was great and many chapters, naturally, do not cut deep. The author's personal interest has been in oceanography, entirely from a descriptive angle. The methods of dynamic oceanography have not been used. 'El Nino', the perturbation of the Peru current which brings death to myriads of fish and sea birds, is examined at length. It seems that much confusion surrounds the term and anyone wishing to use it would be wise to consult this book to find out what it means. The style is friendly and discursive. Anyone in search of a worth-while problem for study may find one on every page. L.H.N.C.

W. H. Searle

J. mar. biol. Ass. U.K. (1960) 39, 417–418
Printed in Great Britain

OBITUARY

William H. Searle, B.E.M.

By the death at the age of 84 of Mr William H. Searle there passed away, on 6 April 1960, one who had served the Laboratory longer than anyone else and who, during his 63 years as fisherman-collector, had installed himself in the affections of countless biologists the world over. From December 1895 until his retirement on 30 September 1958 his assiduous and unwearied devotion to his collecting duties, year in and year out whatever the weather, on the shore or in his boats, earned him the lasting gratitude of all those innumerable research workers, teachers and students who relied on 'Bill' to procure living material for their researches or studies. He, more than anyone else, knew where the animals were to be found, how to capture them without damage and how to ensure their safe arrival at the Laboratory hours later. More than one student who had been collecting on the shore alongside Bill has later been astonished to observe the large and varied assortment of creatures emerging alive and kicking from one small and tightly packed basket. He had a keen eye for the little things—*Gromia*, praniza larvae and the like, from the rock crevices he split open with his crow-bar. These he would carefully transfer from silted rock surface to honey jar on the point of his pocket-knife. He knew well their scientific names, though foreigners would often have difficulty in recognizing them when pronounced with a strong Devonshire accent. It was usually the old names current during his youth that he knew, and he was not alone in deploring the activities of systematists in so frequently changing and re-changing so many of them.

Bill often spoke of the wonderful time he spent with the late Dr E. J. Allen, F.R.S., and the late Mr R. A. Todd exploring, for its fauna, the Salcombe estuary during the summer of 1900, when so much was excitingly new. Collecting trips to Salcombe with Bill, even thirty years later, are still as green in the memory of a younger generation as were then the acres of *Zostera* amid which Bill's fork turned up rare and fascinating things. He was largely responsible for discovering the riches of the rocky reefs at Wembury Point; in those days walking there and back from Turnchapel, no short distance when carrying a crowbar and one or two loaded collecting baskets.

Of the boats he used in Plymouth Sound and immediate environs the small sailing ship 'Anton Dohrn' was worked by him for many years single-handed. He served aboard 'Busy Bee', 'Huxley', and 'Oithona', and from 1923 onwards skippered the motor-boat 'Gammarus'. In those days 'Gammarus' had a stout mast on which with a following wind Bill would hoist sail to help her along, for in her early years she was rather underpowered.

Bill's knowledge of the bottom of Plymouth Sound was unrivalled; legend has it that caught by a sudden sea-fog he could always tell where he was by dredging up a sample of the bottom. Like so many of the older seamen he could not swim, and he chewed, not smoked, tobacco.

Well deserved honours came to Bill late. In 1953 he was elected an associate member of the M.B.A.; he received the Queen's Coronation Medal and in 1957 the British Empire Medal. When he retired he could look back with pride on a long life well spent in the service of science.

D. P. WILSON

J. mar. biol. Ass. U.K. (1960) 39, 419–431
Printed in Great Britain

A MUSCLE RECEPTOR ORGAN IN *ELEDONE CIRRHOSA*

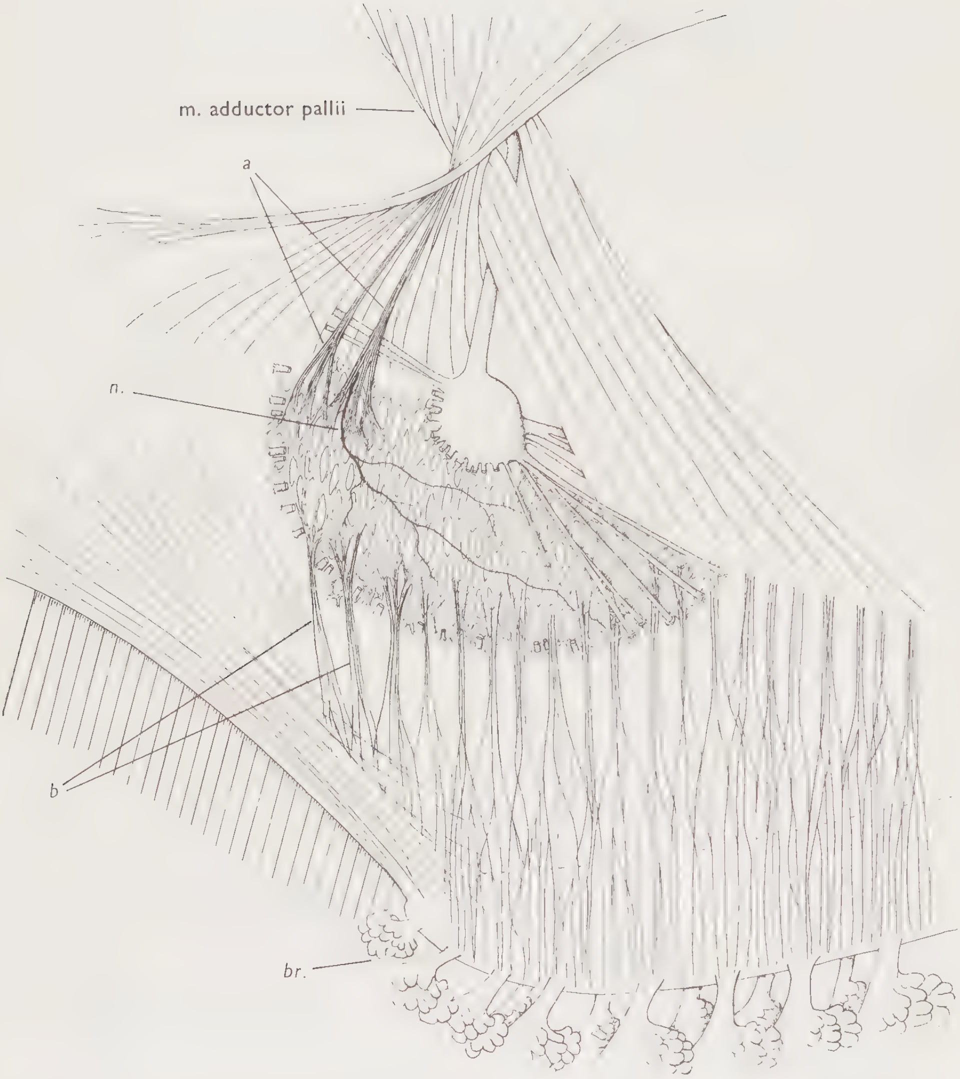
By J. S. Alexandrowicz
The Plymouth Laboratory

(With Plate I and Text-figs. 1–4)

Nerve cells evidently of a sensory nature have been found in *Eledone cirrhosa* on the inside of the mantle in a limited area near the stellate ganglion. The cells, whose number on each side of the body is no less than 50, are in close association with a special thin layer of muscles, and obviously must have a proprioceptive function. The whole complex can therefore be regarded as a muscle receptor which from its situation may be termed the substellar organ.

The muscular component of this organ consists of fibres arranged in very flat bundles which, anastomosing with one another, form a plexiform layer situated under the stellate ganglion and the stellar nerves. It may be called substellar muscle plexus (ss-plexus for short). The area occupied by it, which is roughly semicircular in shape, extends to the points where the stellar nerves penetrate the muscles or a little beyond these points (Text-fig. 1). The ss-plexus, although situated close to the compact muscle of the mantle, does not appear to have anatomical relation with the latter; it has, however, direct connexions with strands of muscle fibres reaching the plexus from two directions. The fibres coming from the median side belong to the muscle attaching the mantle to the visceral sac in which runs the pallial nerve (or mantle connective). This muscle, called lateral pallial adductor (see Tippmar, 1913) is twisted in such a way that its bundles coming from the anterior region of the visceral sac insert into the mantle behind the stellate ganglion, and those originating posteriorly insert in front of it. It is from the latter portion of the muscle that some thin bundles pass into the ss-plexus (Text-fig. 1 *a*). From the opposite side several muscle bundles (*b*) approach the plexus which are part of the thin layer of muscle fibres situated in the membrane attaching the branchia to the mantle. Most of the muscle fibres of this membrane run in the same direction towards the line of insertion of the pallial adductor and the area of the ss-plexus; near the free border of the branchial membrane they form a somewhat thicker band running parallel to this border.

It should be emphasized that a part only of the ss-plexus is connected with the muscle fibres of the pallial adductor and of the branchial membrane. Its other fibres spread in the connective-tissue sheet lining the mantle and terminate in this tissue independently of the neighbouring muscles. On the



Text-fig. 1. *Eledone cirrhosa.* Inside view of portion of the mantle showing the situation of substellar muscle plexus of the right side. Most of the stellar nerves have been cut out to show the plexus connecting with (*a*) the fibres of m. adductor pallii, and (*b*) the fibres of the muscle of the branchial membrane. *n*, nerve to the substellar muscle plexus; *br.*, branchia.

other hand, many fibres of the branchial membrane passing on to the area of the ss-plexus do not fuse with its bundles and insert into the connective tissue in the meshes of the plexus.

The muscle fibres of the plexus which are *ca.* 3μ thick can branch and exchange anastomoses. The mode of their arrangement can be seen in Pl. I, fig. 1.

The ss-plexus is often very distinct in methylene-blue preparations. In order to facilitate its staining it is advisable to remove the epithelial layer lining the mantle cavity, to cut out the stellar nerves and to take away carefully the loose tissue beneath them. For better observation of the muscle and nerve elements the plexus can be separated from the mantle wall, but this should be done when the preparations after staining, fixing, etc., have been transferred into xylol. One must proceed from the outside, taking piece by piece the mantle muscles from the plexus and not vice versa. Preparations shown in photographs (Pl. I) were made in that way. The muscle fibres stain with methylene blue readily but unevenly. Much better pictures of the plexus structure can be obtained with Bodian's method; in such preparations, however, it is much more difficult to remove the unwanted tissues from the plexus muscles.

Nerves

The nerve supplying the plexus muscles arises from the mantle connective. It is covered at its point of origin and in its initial course by that portion of the pallial adductor which passes in front of the stellate ganglion. After giving off to this muscle several branches the nerve emerges near one of the bundles fusing with the plexus and runs across the latter in a wavy line obliquely backwards distributing branches to the muscles. In addition to this system of nerves which are doubtless of motor character there is on the plexus a second system connecting with some of the stellar nerves by thin nerves. The greatest number of the latter was four in one preparation, but how many they actually are remains uncertain. They are difficult to find for they join thinner stellar nerves situated deeper under the thick ones, and as the space between the stellar nerves is filled by loose tissue which must be removed one can never be sure whether in this operation some tiny nerves have not be torn away. On the other hand, there are here thin arteries which can easily be mistaken for nerves.

It seems very probable, as will be shown below, that this system of nerve fibres is formed by the axons of receptor neurons.

Nerve cells

Nerve cells are scattered over the ss-plexus at a distance from one another; sometimes two or, more rarely, three can be seen lying close together. They are all multipolar and can have a variety of shapes depending on the disposition of their processes (Pl. I, figs 3–5). Owing to this feature their dimensions can only be generally defined as being in the range between 40 and 100μ. How many nerve cells there are in all on the plexus could not be exactly determined because they are difficult to stain: sometimes they do not show at all, in other instances only a few can be spotted. The greatest number seen in one preparation was 25 in an area approximately equal to half of the plexus. Hence it may be deduced that their total number is not less than 50, but it can be higher than that. Because of their poor staining properties it has not been possible to gain a precise knowledge of their distribution. Such pictures as in Pl. I, fig. 2, showing several cells not far from one another, are not often seen, and there is no certainty whether the cells are spaced in the same way on the whole plexus. It is true that groupings with similarly or even more densely arranged cells have been observed at various points near the central region of the plexus as well as towards its periphery, but there is still not sufficient evidence whether the cells are distributed so closely everywhere or merely at certain points.

The number of processes arising from cell bodies is variable. Five or six of them are usually met with, but their true number can be greater since in addition to the thick processes some tiny ones can be frequently noticed, but they do not stain well. The processes which must be classified as dendrites project in all directions giving off branches spreading on the muscles. The thicker of them cross the muscle bundles at various angles, whilst the thin ones take their course alongside the muscle fibres. Very thin branches can arise directly from the stout cell processes, sometimes several of them close to each other. No special end-organs could be seen, and whether the nerves terminate on the muscle fibres or on the connective tissue between them I am unable to say.

The cell processes can be followed in favourable conditions for about 250μ from the cell body, but appear not to end there, at least not all of them. Their tracing in methylene-blue preparations is uncertain because of the difficulty in distinguishing the nerves from the muscle fibres that stain readily and give off fine branches frequently looking like nerve filaments. There are, moreover, on the same muscles, motor fibres coming from the nerve mentioned above. Besides, methylene-blue preparations are often indecipherable because of deformations of fibres produced by longer immersion of tissues (8–10 h, sometimes up to 20 h) in methylene-blue solution in sea water

EXPLANATION OF PLATE I

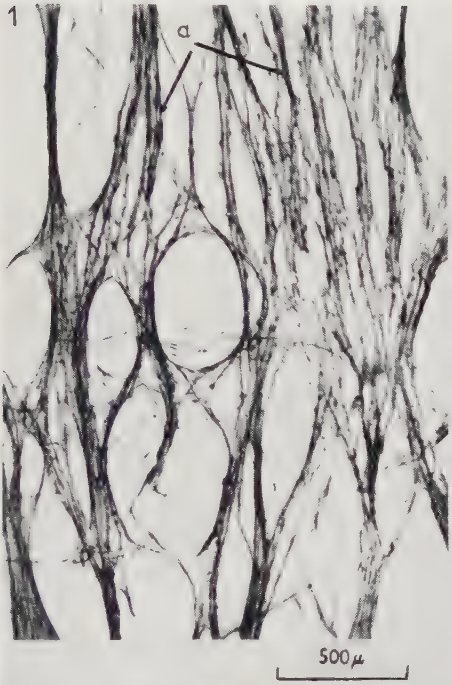
All photographs were made from preparations of *Eledone cirrhosa* stained with methylene blue, fixed in ammonium molybdate and mounted in xylol-dammar.

Fig. 1. Substellar muscle plexus. *a*, bundles of fibres coming from m. adductor pallii.

Fig. 2. Receptor cells (indicated by arrows) on the substellar muscle plexus.

Figs. 3–5. Receptor cells of various shapes.

1



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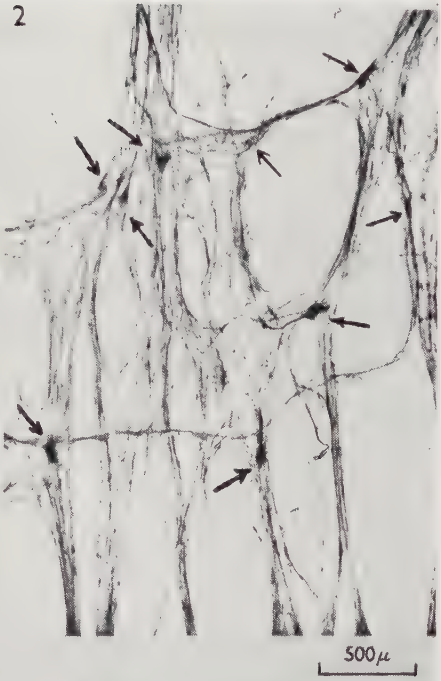

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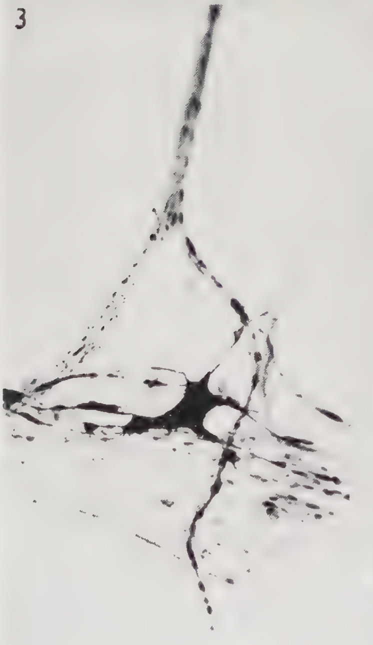

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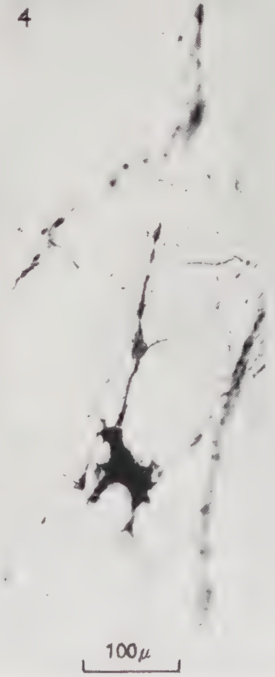

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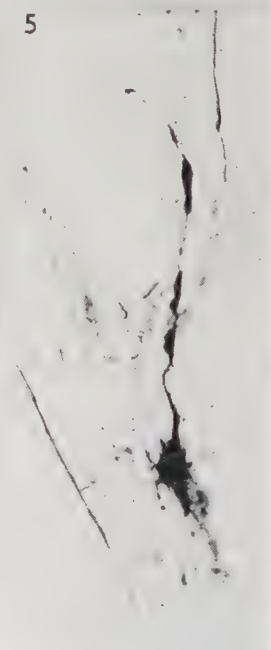

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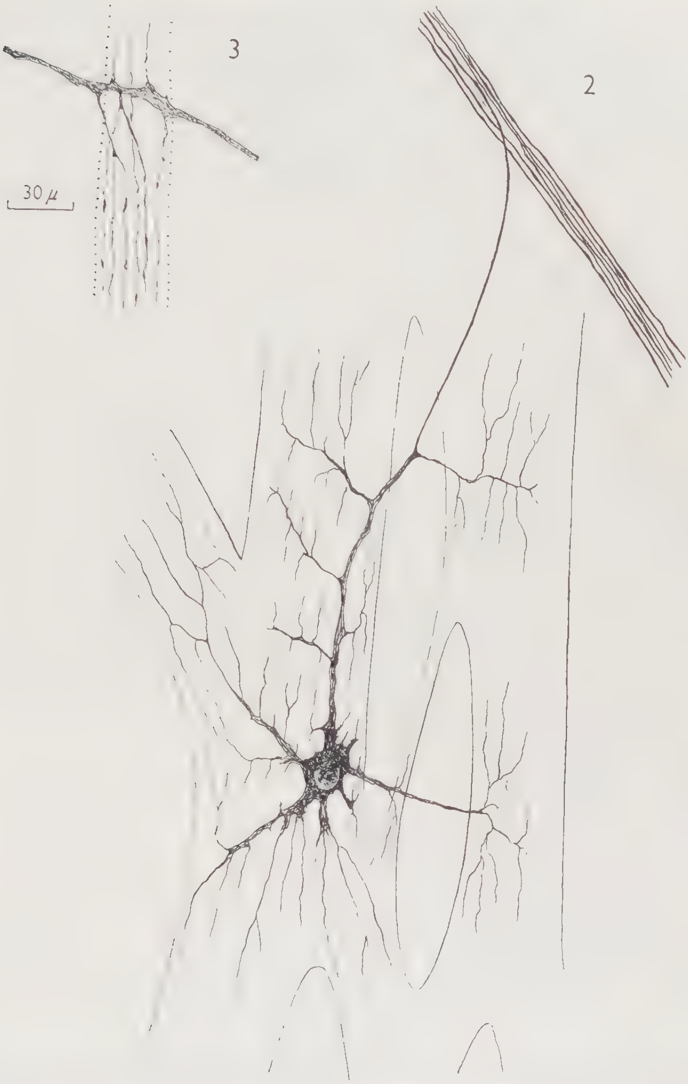


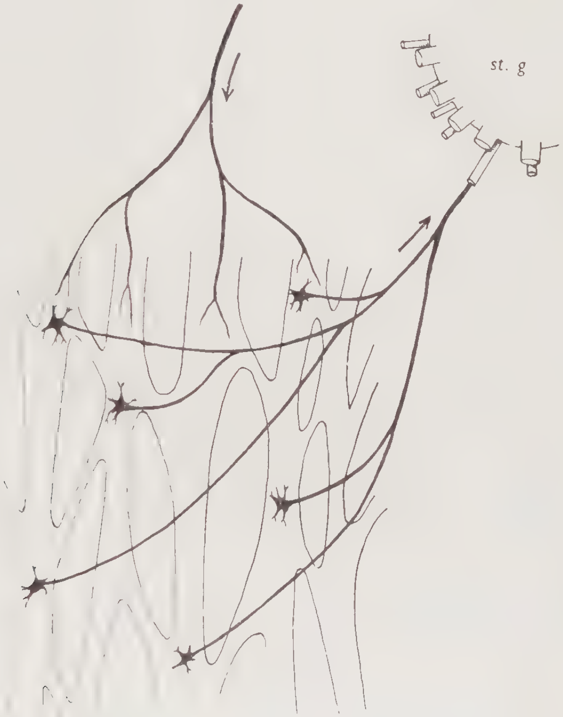
Text-fig. 2. Receptor cell of the substellar organ. Drawing compiled from several preparations.

Text-fig. 3. Fine branches of a receptor cell dendrite given off to a small strip of plexus muscle (outlined by dots). From preparation stained with Bodian's method.

(1:30,000). The dendritic processes proved to be particularly susceptible to this treatment and disintegrated readily. More reliable pictures have been obtained with Bodian's method which proved to be helpful in determining (on whole mounted preparations) the course of the cell processes and their finer branches. The representation of the receptor neuron shown in Text-fig. 2 is based on pictures obtained with both staining methods. It may be that the expansions of some dendrites reach farther than seen in this drawing, and it must be realized that the fine terminal branches are much more numerous than is shown. How dense they in fact are can be judged on the evidence of preparations in which the impregnation of some branches was more complete. In Text-fig. 3 is shown a muscle strip only 32μ wide crossed by a cell process which sends to this muscle several branches running parallel with each other and obviously destined exclusively to this muscle strip. Although such pictures, because of uneven impregnation of nerve elements, are not of common occurrence, there is every reason to believe that in the dendritic field of each neuron the nerves fibres are in similar relations with the muscles. Furthermore, considering the length of the cell processes and the distribution of the nerve cells, it may be assumed that in those regions where the nerve cells are situated not far from one another all muscle bundles are covered by their processes. Should the cells be equally densely spaced over the whole ss-plexus then the latter would be everywhere pervaded by the ramifications of their dendrites.

The axon at its root and in its initial course is not easily discernible since it gives off branches looking exactly like those of the dendrites. Occasionally it stains better than the other processes and then can be recognized at first sight (Pl. I, fig. 5). When the processes stain equally well it can sometimes be distinguished by its greater thickness, but this is not a reliable characteristic. Thus, the identification of the axon can only be certain when it is possible to trace it for a longer distance. It can be then seen that its outlines are somewhat uneven up to the point at which branches cease to spring from it. When the last of these branches is given off (this point can be at a distance of about 500μ from the cell body), the axon changes in appearance and proceeds farther as a smooth fibre which finally joins one of the nerves running on the plexus. Sometimes three or four axons associate and run together before entering a thicker bundle of fibres. In a few cases when such a nerve carrying the axons could be followed in its proximal course it was found to join one of the thinner stellar nerves. This observation revealed the existence of connexions, already alluded to, between the nerves of the plexus and the stellate ganglion and provided indicative evidence as to the course taken by the axons of the receptor cells. Whether they all behave in the same way is difficult to ascertain because the nerves on the ss-plexus run in all directions anastomosing occasionally with each other, and the tracing of fibres of different origin is possible in exceptional cases only. Anyhow, in view of the evidence available it seems more probable that the centripetal paths of these receptor cells are directed towards the stellate ganglion. According to this assumption the basic pattern of nerve elements in the substellar organ would be as diagrammatically represented in Text-fig. 4.

In *Octopus vulgaris* the structure of the ss-plexus was found to be essentially the same as described above, and the presence of nerve cells in it could be ascertained. Therefore the substellar organ in this species appears to be quite similar to that in *Eledone*, but, as I examined one specimen only and more material was not available, the present account had to be restricted to a single species of the Octopoda.



Text-fig. 4. Simplified diagram of the arrangement of nerve elements in a part of the substellar organ. *st.g.*, stellate ganglion.

DISCUSSION

It is evident that the nerve cells in the substellar organ are of a sort differing markedly from all known types of cells in other organs of cephalopods. On account of their position in a muscle layer a comparison might be made with the ganglion cells of the nerve plexus in the digestive tract and those in the auricles. However, the former are unipolar or bipolar and only rarely tripolar, and evidently it is not their dendrites, but their axons, which are spreading over the muscle fibres. The cells in the auricles are unipolar and are doubtless of a different sort (Alexandrowicz, 1928, 1960). As regards the mantle muscles there is only one reliable record of the presence of multipolar cells in them, viz. in the paper of Sereni & Young (1932), in which a photograph is reproduced showing a section through the mantle muscles with such nerve cells stained after Cajal. If these sections were made, as seems very probable, from the region of the mantle under the stellar nerves, the cells found in them would be doubtless the same as described in the present paper, for, as Young states, they were situated 'in the thin coats of muscle cells which lie outside the main mass of muscles' which might well be the substellar muscle plexus. In the above-mentioned paper dealing with degeneration and regeneration of nerves the question of these nerve cells is not pursued further. Young briefly states that 'they have very many branches some ending near the cell others running for long distances along the muscle fibres against which some of them seem to end'. He mentions also the observations of Mikhailoff (1921), but the work of this writer is of such a kind that it can be ignored in the present discussion.[1]

[1] Mikhailoff's claims have been taken at their face value by many writers and reproductions of his drawings can even be found in several books. It is understandable that the authors of synoptic works are not in a position to assess the value of the assertions of each writer and consequently some fallacies can drag on through the scientific literature. I consider it my duty, however unpleasant, to expose one of such cases.

Mikhailoff affirms to have discovered an ubiquitous system of peripheral nerve cells in the muscles and various organs of cephalopods. In his words: 'Les cellules nerveuses périphériques sont disséminées en plus ou moins grand nombre presque partout. Quelquefois elles sont solitaires, quelquefois elles constituent de petits ganglions à 5–30 cellules.' He assumes that they occur in all muscles, but one region only in which they were observed is somewhat more exactly indicated. 'Entre les couches musculaires externes du corps ces cellules nerveuses se localisent autour de la tête de l'animal à quelque distance de celle-ci, en constituant le véritable collier, parcequ'elles sont associées à l'aide de leurs prolongements nerveux. De ce collier ou cercle partent 16 chaînettes, dont huit se localisent dans la musculature du corps et les huit autres—dans les bras, par une chaînette à chaque bras.' In order to verify what this intriguing system might be, I tried to stain it with methylene blue in *Sepia* and could easily find the 'chaînettes' in the arms. They are nothing else but the components of the complicated innervation of the arms described by Guérin (1908). There are in fact several such peripheral nerve trunks in each arm called by Guérin (not quoted by Mikhailoff) cordons (or chaînes) nerveux intramusculaires. Mikhailoff's 'collier ou cercle' was most probably the ring formed by commissures between the arm nerves known already to Cuvier and represented in all the works dealing with nervous system in cephalopods. The other eight nerves connecting with the 'collier' could have been the main arm nerves which Mikhailoff did not follow to their origin in the brachial ganglia and assumed that they pass on to the muscles of the body. If therefore, as it is evident, his belief to be a discoverer of new nerve elements in the muscles and his ideas about their structure were chiefly, or perhaps entirely, based on the observation of the peripheral trunks in the arms, they resulted from the basic ignorance of the anatomy of the animals investigated. What structures he saw in other muscles and considered them to be nerve cells is difficult to say. His statement that the size of these 'cells' was 4–9 μ makes the supposition probable that they were swellings produced on fibres during staining since the nerve cells in cephalopods are as a rule much larger and even the smallest of them measure more than 10 μ.

As regards other organs mentioned by Mikhailoff his remarks about the presence of nerve cells in the heart and 'certain glands' are very vague and hardly trustworthy. What, however, he saw in the intestine were true nerve cells, but, first, their presence in this organ was already known and, secondly, his description was inadequate.

No importance whatsoever can be attributed to Mikhailoff's classification of nerve cells (motor, sensory, trophic), based on structural differences of their processes as he saw them.

The first question which arose when the nerve cells on the ss-plexus were noticed was that of their nature and this was really puzzling as long as it was not evident how the cell processes that ended on the muscles and seemed to be all of the same kind should be classified. After it had been ascertained that each cell possesses one long projection joining a nerve trunk it became clear that the others are dendrites and that the basic structure of these neurons is that of typical units of the nervous system. Nevertheless they are remarkable in many respects.

The fact itself that such sensory cells with their dendrites terminating on muscles are present in cephalopods is interesting because elements of a similar sort have been found in a small number of animals, and in those in which their presence is known, as in crustaceans and insects, they occur in a very limited number and only in particular regions of the body.

Compared with the muscle receptors in crustaceans the substellar organ in *Eledone* shows important differences in the way in which the muscular and nervous components are connected with each other. In the former the arborizations of the nerve cells end in a special region of the muscle in which the muscle tissue is replaced by connective tissue fibres, whereas in the substellar organ the branches of the dendrites spread over the wide areas of the muscles. Perhaps the enigmatic N-cells in thoracic muscles of some crustaceans show certain points of resemblance in the behaviour of cell processes since they have processes of considerable length running in various directions and terminating between the muscle fibres; however, the pattern of distribution of their terminal branches is different and their dendritic fields are limited to a small part of the muscle unit.

The presence of branches springing from the axon, but looking and behaving like the processes of the cell body, is a striking but not unknown feature. Similar processes from the axons have been found in sensory cells of insects (Zawarzin, 1912), in the cells of muscle receptor organs and N-cells of decapod crustaceans, and in certain sensory cells of stomatopods (Alexandrowicz, 1952, 1957).

A peculiar feature of the substellar organ which puts it into a special

He obviously exercised little criticism in interpretation of methylene-blue preparations and considered various artefacts to be distinctive features of nerve elements. Artefacts in Mikhailoff's preparations were presumably even more frequent than usual since he applied very hypotonic solutions (equivalent to 0·9 % NaCl), because, as he affirms, solutions of methylene blue in sea water or isotonic liquids are unobtainable. This is proof that not a single work of various writers who applied such solutions for staining the nervous system in marine invertebrates was known to him. There is indeed no reference to any work relating to the subject of his investigations. There is instead a list of the writer's own papers concerning the nervous system of vertebrates.

Thus, there can be no doubt that all Mikhailoff's claims were unfounded. At the best he can be credited for having given, although unintentionally, pictures of peripheral nerve trunks in cephalopod arms stained with methylene blue (his fig. 1 and evidently fig. 8), whereas their previous representation by Guérin was based on Golgi preparations.

category of muscle receptors is the multitude of neurons connected with its muscular component. In crustaceans a receptor consists as a rule of one cell and one muscle. In insects a similar basic pattern of structure of muscle receptors has been found (Finlayson & Lowenstein, 1955; Slifer & Finlayson, 1956). It is true that in some instances a fusion of receptor muscles can take place, as for example, in *Leander serratus* (Alexandrowicz, 1956) and *Praunus flexuosus* (unpublished observation of the writer), so that several nerve cells (up to 4) can end on one long muscle. The fact, therefore, that several cells are in relation with one muscle is not unique, but it is their number in the substellar organ that is striking. Considering the structure of this organ it does not seem probable that it could be functionally differentiated since to the best evidence the ss-plexus appears to be an anatomical unit. This would imply that the changes in condition of the plexus such as occur during contraction or stretching must affect all its muscle elements at the same time. Consequently, whichever of these changes is eliciting the response of the receptor cells the latter must be triggered simultaneously. It follows that when the receptor organs of the two sides of the body react together, as they probably do, the impulses to higher centres are transmitted by one hundred neurons at least.

The accumulation of so many nerve units in one organ may perhaps find its explanation in the fact that in cephalopods in general the number of neurons involved in innervation of any organ is comparatively much greater than in arthropods. I have already (1960) pointed out this 'uneconomical use of nervous substance' when discussing the abundance of nerve elements in the hearts of *Sepia*.

As regards the function of the substellar organ, the only conclusion which can be drawn from the histological evidence is that just mentioned, namely, that it responds to changes affecting the plexus muscles and, since the latter are connected with the pallial adductor and the muscle of the brachial membrane, the function of the receptor must also be related to the action of these muscles. It is, however, not obvious whether the receptor cells become stimulated by the contraction or by stretching of the plexus muscles. It is equally difficult to guess whether these organs are in action only during vigorous contraction of the mantle muscles such as occur when the animal swims backwards, or play some role in adjustment of respiratory movements varying in intensity.

The assumption that the axons of the receptor cells run towards the stellate ganglion harmonizes with the results of Young's experiments (Sereni & Young, 1932) on degeneration and regeneration of fibres in the stellar nerves and the mantle connective (in *Eledone* and *Octopus*). Young came to the conclusion that there are in these nerves 'afferent fibres whose cell bodies lie at the periphery'. He even mentions that this path of afferent fibres may include possibly a few proprioceptors.

There is every reason for assuming that the axons of substellar receptors would behave like those in Young's experiments, but it is not evident whether the afferent path discovered by him consisted of these elements only. Young defines it as 'small' and referring to the afferent fibres in the stellar nerves says that 'they are very few in number compared with the motor fibres'. It is therefore possible that they could all come from the substellar organ; some other considerations, however, make this supposition questionable. My observations of the course of cell axons do not tally well with Young's results on one point. As stated in the foregoing description the axons of the receptor neurons appear to join the stellar nerves of thinner calibre, whereas the afferent fibres observed by Young were evidently running in the thick trunks, as he explicitly states: 'such fibres seem to be more numerous in the large posterior stellar nerves than in the lateral ones'. There are two possibilities: either some nerves carrying the receptor axons and joining the thick stellar nerves were not noticed by me—they could easily be torn away when removing the connective tissue between the nerves—or there is another system of fibres running into stellate ganglion from some yet unknown sensory cells. As these afferent fibres were apparently seen in many thick nerves the second alternative appears to be more probable. The conclusive evidence could possibly be provided if Young's experiments were repeated with the aim of estimating the number of afferent fibres in the stellar nerves. If it were found that this number in the stouter of these nerves surpassed their possible number from the substellar organ, there would only be the question where these other sensory cells sending their axons through the stellar nerves are situated. It would be also interesting to know where the axons of the receptor neurones of the substellar organ are ending. Young proved that there is a path of centripetal fibres in the mantle connective and concluded that the afferent fibres from the stellar nerves pass through the stellate ganglion. The question is whether or not some of them terminate in this ganglion. Here perhaps the comparison of the number of fibres entering the ganglion with the stellar nerves and leaving it with the mantle connective could provide some evidence.

Are there proprioceptors of a similar or of some different kind in other species of the Cephalopoda and in other regions of their body? Considering the high degree of development of the nervous system in these animals and the richness of nerve elements in all their organs it seems plausible that if in the neuromuscular mechanisms of vertebrates and arthropods the proprioceptors play an important role, the cephalopods should have them also.

In many attempts to solve this problem I examined various regions of the cephalopod body, paying special attention to those muscles which at certain movements of the animal become more forcibly stretched, on the supposition that in such muscles the proprioceptors are more likely to occur. This conjecture was based on the fact that the stretch receptors in crustaceans associated with the extensor muscles must become stimulated at the flexion of the abdomen. As one sort of these receptors (MRO 2) presumably responds to strong contractions of the flexor muscles, such as during the flipping of the abdomen in escape reaction, I ventured to suggest (1951) that its function may consist in inhibiting the giant fibres after each powerful contraction of the muscles produced by them. On this line of thought the occurrence of muscle receptor organs was rather to be expected in decapod Cephalopoda which have giant fibres, but the search for them in *Sepia* and *Loligo* has been as yet unsuccessful. This is not to say that they are in fact missing, and neither can it be maintained that in Octopoda they are present in that region only where they have been found. If their structure should be of a similar type as in the substellar organ this would add to the difficulties of research. A thin muscle unit with different pattern of innervation as in MRO of crustaceans can be often clearly distinguished amidst the ordinary muscle fibres even when the nerve cell does not show. If, however, the receptor organ should consist of nerve cells connected with muscles of common appearance, and these cells were refractory to staining, their discovery would depend on such a chance, as happened in the present case with *Eledone*, that a nerve cell was spotted and efforts could be concentrated on one region.

The conclusion to be made is that, since negative results have no value, the problem of the absence or presence of receptor organs in cephalopods cannot be solved until some infallible method of detecting nerve cells is found and with the aid of such a method the whole muscle system is submitted to systematic investigation.

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SUMMARY

In *Eledone cirrhosa* a muscle receptor organ has been found situated under the nerves radiating from the stellate ganglion. This organ for which the term substellar organ is proposed consists of nerve cells scattered over a plexus of muscle fibres connected with the bundles of the pallial adductor muscle and of the muscle of the branchial membrane. The nerve cells whose number is no less than 50 on each side of the body are multipolar with long dendritic processes sending many thin branches alongside the muscle fibres. The axons of these receptor neurons join the stellar nerves and run in them towards the stellate ganglion. Whether all the axons of these neurons take the same course and where they end could not be ascertained.

The motor innervation for the muscular component of the substellar organ is supplied by a nerve arising from the mantle connective (pallial nerve).

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PLANT HORMONES IN MARINE PHYTOPLANKTON, ZOOPLANKTON AND SEA WATER

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(Text-figs. 1–4)

Studies by many workers on the subtle ecological relationships of marine organisms suggest that the distribution of these organisms may be controlled, at least in part, by trace organic substances in their environment. These substances may range from 'toxins to vitamins and hormones' (Lucas, 1955). Saunders (1957) has reviewed the interrelations of dissolved organic matter and phytoplankton and considered the possible roles of organic metabolites in the growth of the algae. The presence of several vitamins, for example, B_{12}, thiamin, niacin and biotin, has been demonstrated in natural waters, but the possible occurrence of plant hormones has not previously been considered.

Work is in progress at Aberdeen on the production by algae of plant hormones of the auxin type, and detection of these auxins in algal media. Auxins are hormones which promote cell enlargement in plants. All the known auxins are indole compounds. This paper reports results of an examination of marine phytoplankton and sea water.

Many of the indole compounds known to be concerned in the bio-synthesis or degradation of indole auxins in the higher plants also occur in animals. For this reason it was decided to examine also zooplankton.

MATERIALS

The following materials have been examined:

Plankton

Marine phytoplankton and zooplankton collected by the fisheries research ships of the Department of Agriculture and Fisheries for Scotland was treated immediately on collecting with half its volume of ethanol, and stored in the deep-freeze or freeze-dried on reaching the laboratory.

Details of the phytoplankton samples, which consisted predominantly of diatoms, are given in Table 1. In addition to the species listed in Table 1, a few protozoa, silico-flagellates, small copepods and faecal pellets were present in sample I, a few faecal pellets in sample II and a few dinoflagellates in all three samples.

TABLE 1

Species	Cells/litre			
	I	IIA	IIB	III
Leptocylindrus danicus	120	—	150	—
Chaetoceros debilis	120	195	750	—
C. decipiens	105	135	1350	—
C. convolutus	—	—	600	—
Thalassiosira gravida	75	15	—	—
Guinardia flaccida	45	—	—	—
Nitzschia seriata	45	45	1500	1080
Coscinodiscus concinnus	45	—	—	—
Thalassiothrix longissima	45	—	—	—
T. nitzschioides	30	—	—	—
Rhizosolenia hebetata (semispina)	—	90	2700	—
Rhizosolenia styliformis	—	—	—	405

All hauls were by vertical standard net. Trawling positions were as follows: sample I, 60° 35′ N., 3° 12′ E. 14. iv. 57; IIA 57° 00′ N., 1° 00′ W. 31. v. 57; IIB 66° 47′ N., 16° 27′ W. 18. vii. 57; III, 60° 31′ N., 0° 40′ W. 8. vii. 58; 59° 3′ N., 2° 15′ W. 11. vii. 58.

Zooplankton sample I consisted predominantly of Copepoda (*Temora*, *Calanus*, stages I–IV and *Para/Pseudo-calanus*) and sample II predominantly of a mollusc, *Spiratella* (*Limacina*) *retroversa*. The trawling positions were as follows: sample I, 55° 5½′ N. 5° 2′ W., 2 May 1958; sample II, 61° 1′ N., 10° 0′ W., 10 July 1958.

Sea water

(I) 110 l., from 60 miles off-shore (57° 0′ N., 0° 30′ E.).

(II) 200 l., inshore sea water collected along the east coast of Scotland just south of Aberdeen.

EXPERIMENTAL TECHNIQUES

Slightly different extraction techniques were used with the different materials, and full details are given below. Attention is concentrated in this paper on the following fractions: (1) the acidic ether-soluble fraction (EA fraction), which would contain 3-indolylacetic acid (IAA) and most of the known auxins if present; (2) the acidic ether-soluble substances derived from the hydrolysed aqueous ether-insoluble fraction (SA fraction); and (3) the corresponding neutral fractions (EN and SN).

Some explanation of the reasons for examining the second set of fractions may be desirable. Recent work on plant growth hormones has shown that significant amounts of biological activity occur in the aqueous, ether-insoluble fractions of plant extracts, a fact which is of considerable interest, as the activity cannot be explained in terms of any of the known hormones. It was important therefore to analyse this fraction. Unfortunately, a direct examination is difficult, because large quantities of pigments, carbohydrates, amino acids and other substances, which may interfere with the bio-assays, are present. The following procedure was therefore adopted.

From an analysis of previous work on the aqueous, ether-insoluble hormones it is possible that these substances are unstable auxin complexes which yield ether-soluble hormones on treatment with acid or alkali (Bentley, 1960*a*). Accordingly, it was decided to treat the ether-insoluble fraction with alkali and look for any ether-soluble hormones produced. If any were found, they would be much more amenable to examination than substances in the aqueous ether-insoluble fraction, and it was hoped that any results obtained with them would help to shed light on their non-ether-soluble precursors. This fraction is referred to as the saponified fraction (SA = saponified acidic; SN = saponified neutral).

Detailed extraction techniques

Phytoplankton sample I

The material, which had been stored in the deep-freeze without filtration, was acidified to pH 5·0 and stirred for 30 min with 500 ml. absolute ethanol. The mixture was filtered through paper pulp and the alcohol extract neutralized. The alcohol was removed under vacuum leaving 70 ml. aqueous extract. This was re-acidified to pH 5·0 and extracted with ether. The ether extract was divided into acidic (EA) and neutral (EN) fractions, using 5% $NaHCO_3$. The aqueous, non-ether soluble material, was saponified with N-NaOH for 30 min at 15 lb. pressure, acidified and extracted with ether. This saponified extract was also separated into acidic (SA) and neutral (SN) fractions.

Phytoplankton sample II

The samples were freeze-dried on arrival in the laboratory (dry weight 5·4 g). A little water was added, the pH adjusted to 5·0 and the mixture stirred for 30 min with two lots of 100 ml. chloroform. The material was filtered and separated, the chloroform fraction washed free of HCl, evaporated to dryness and extracted with light petroleum 40–60 °C to remove fatty materials. The petroleum fraction was rejected. Extraction with three lots of methanol followed, the methanol extract evaporated to dryness, the residue taken up in ether and split into acidic (EA) and neutral (EN) fractions. The aqueous non-chloroform soluble fraction was extracted with petroleum, then saponified as sample I and split into acidic (SA) and neutral (SN) fractions.

Zooplankton samples I and II

The material was extracted with 80% ethanol in a Waring blendor at pH 4·0, filtered and pH adjusted to 7·0. The alcohol was removed under vacuum, the extract re-acidified (pH 5·0) and extracted first with 40–60 °C light petroleum, then with ether. The ether solution was split into acidic (EA) and neutral (EN) fractions. The aqueous non-ether soluble fraction was saponified and split into acidic (SA) and neutral (SN) fractions.

Sea water

The samples were filtered, acidified to pH 5·0 and extracted by stirring for 1 h with freshly distilled chloroform. The chloroform was separated off, distilled *in vacuo* and the residues extracted with ether. The ether from sample II was separated into acidic (EA) and neutral (EN) fractions. It was not possible to work with the aqueous non-ether soluble fractions because of their large volumes, and because of the high concentration of salts.

Chromatography

Ether extracts were evaporated to dryness on a freeze-drier and the residues dissolved in a few drops of ethanol for loading on to chromatograms. Extracts were usually purified by preliminary paper chromatography using water as eluant and applying the extracts as a broad strip on the starting line; the pigments remained on the starting line, which was rejected. The remainder of the paper was flushed with ethanol and the recovered material chromatographed in *iso*-propanol:water:ammonia (sp.gr. 0·88) (10:1:1), or water. The ammoniacal *iso*-propanol mixture is widely used in auxin chromatography, as it has been found to give good separation of acidic auxins (Stowe & Thimann, 1954). It has the disadvantage that the ammonia may cause breakdown of unstable compounds with production of artifacts (Bentley, 1958*b*, 1960*b*), but it was felt advisable to use it here for the purposes of comparison with earlier work on plant extracts. Water, which was also used, is a neutral innocuous solvent in which the extracts run very quickly, thus minimizing the possibility of breakdown of compounds during chromatography. It was used as a check on the number of active zones obtained in the ammoniacal *iso*-propanol. It has the disadvantage that it does not give good compact spots suitable for colour tests. Some experiments were also tried using *iso*-propanol-water-acetic acid, but under these conditions no separation of active zones was achieved and activity was detected only at the solvent front. Acidic solvent systems were not therefore suitable. Chromatography was carried out in a constant temperature room at 15° C. Chromatograms were examined under filtered ultra-violet light (2537 Å transmitted) and used either for indole colour tests or bio-assays. The reagents used for colour tests were Ehrlich (*p*-dimethyl aminobenzaldehyde), Salkowski and nitrous/nitric acid, using the techniques of Jepson (1958). Chromatograms to be bio-assayed were cut into ten equal portions and the portions eluted with 1 ml. water for testing. 3-Indolylacetic acid (IAA) and 3-indolyl-acetonitrile (IAN) were run as marker spots.

Assay technique

The *Avena* coleoptile straight-growth method, which is a measure of auxin activity in cell-enlargement, was used. 10 mm lengths of *Avena* coleoptiles are suspended in the solutions to be tested, and the increase in lengths measured after 24 h. The tissues grow by cell-enlargement. 1% sucrose and phosphate-citrate buffer (10^{-2} M K_2HPO_4 and $0·5 \times 10^{-2}$ M citric acid) at pH 5·0 is used as a basic medium. For full details of the assay method see Bentley & Housley (1954). The test is specific for auxins. Other growth substances, e.g. vitamins and gibberellins, are virtually inactive. All the chromatography papers used in the bio-assays were washed in water and acetone before bio-assay, to remove impurities. Blank chromatograms, loaded with ether or alcohol but without extracts, were frequently developed and bio-assayed, and showed no biological activity.

RESULTS

Marine phytoplankton

There is an active zone (Z) on the EA chromatograms and hints of activity at two less mobile zones (X and Y, Fig. 1 A). There are also two active zones in the SA fraction (Fig. 1 B), from which all the ether-soluble hormones had been removed before saponification. Several positive Ehrlich colours were obtained with the SA fraction, as indicated, but none with the EA fraction. For the sake of clarity, the three zones of activity in both the EA and the SA fractions in all the species examined have been called X, Y and Z, as indicated on the figures. This is because they show certain points of resemblance with auxins located in other plant materials and labelled X, Y and Z. This work is considered later in this section.

Three zones of activity can also be located in the SA fraction of sample II (Fig. 1 C). It is frequently found that sometimes only one zone (X) can be located; sometimes this can be resolved into two zones (X and Y). These separations probably depend on small differences in conditions of chromatography. A pink (or purple) Ehrlich reaction at R_f 0·1–0·2 has been obtained with all the SA samples examined, as shown in Figs. 1 A and B. This colour reaction indicates the presence of an indole compound. The SA fraction of sample III gave exactly similar results to Fig. 1 C, with three clear-cut zones, X, Y and Z. Thus, it seems that there are at least two, and often three active compounds in the SA fractions of varied samples of phytoplankton, indicating that these compounds are possibly involved in basic metabolism common to a range of species.

It has been thought in the past that the plant hormones were all acidic in nature. However, evidence is accumulating that there are also neutral auxins. Fig. 1 D shows that there is activity in the EN fraction of sample II, though this has not resolved into clear-cut zones. Moreover, it is not always obtained, suggesting that, when it does occur, it comes from neutral precursors, depending on the conditions of chromatography. Figs. 1 E and F illustrate activity found in the SN zones of samples I and II, respectively. Again, this activity is not always obtained and activity in specific zones is not reproducible.

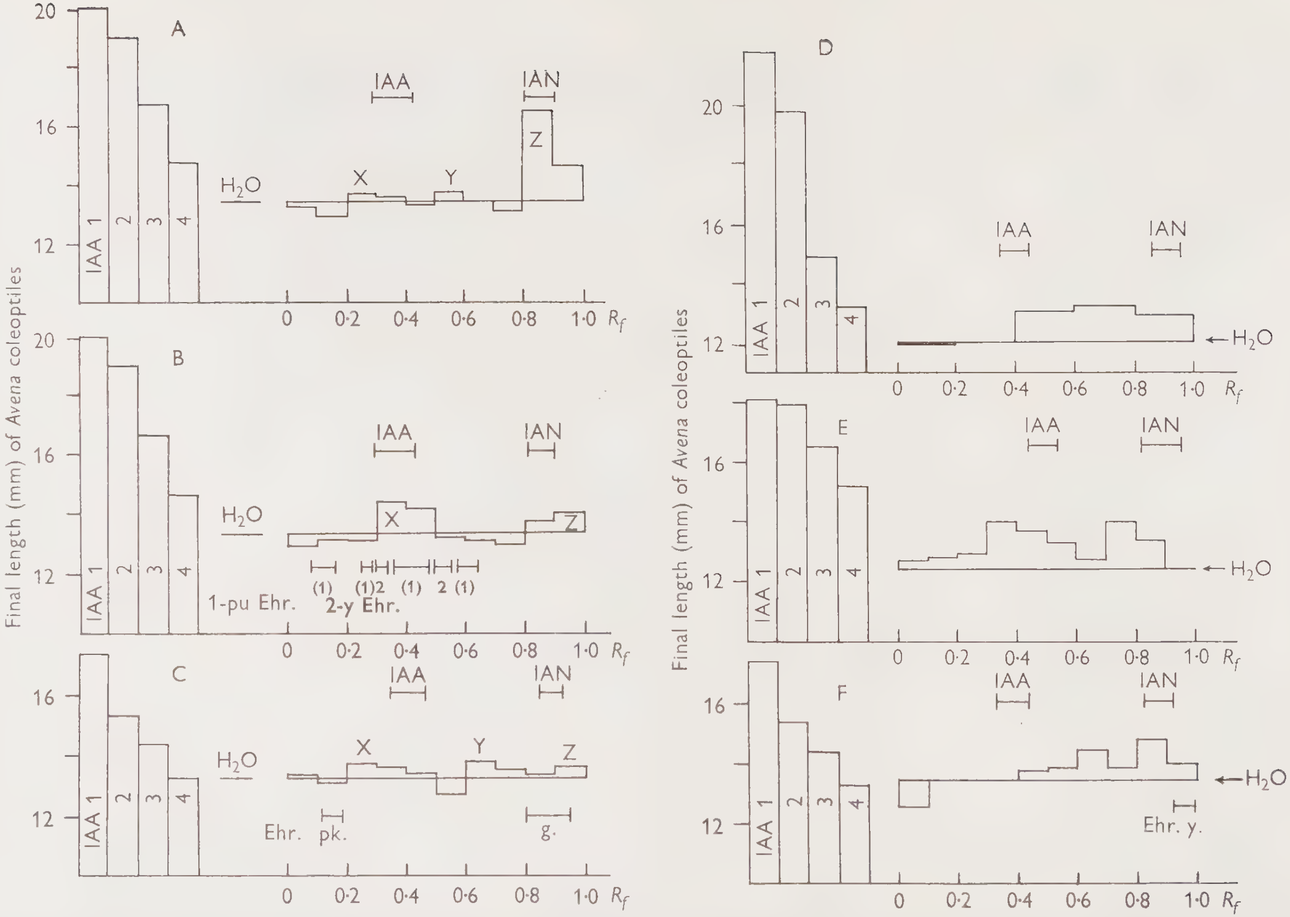

Fig. 1. Extracts of marine phytoplankton chromatographed in *iso*-propanol-ammonia. A, EA fraction of sample I; B, SA fraction of sample I; C, SA fraction of sample II; D, EN fraction of sample II; E, SN fraction of sample I; F, SN fraction of sample II. IAA controls are as follows: 1 = 1 mg/l.; 2 = 0·1 mg/l.; 3 = 0·01 mg/l.; 4 = 0·001 mg/l. Ehrlich colours are as follows: pu., purple; pk., pink; g., green; y, yellow.

The compounds located in the EA and SA fractions show some properties in common, suggesting that in fact they may be the same compounds occurring in both fractions, existing naturally in small quantities and also released possibly from precursors in the aqueous fraction by the saponification. For example, when zone Z in the EA fraction is eluted and re-chromatographed in *water* two active zones appear (Fig. 2 A). When zone X of the SA fraction is eluted and re-chromatographed in ammoniacal *iso*-propanol, activity appears also in zone Z (Fig. 2 B). This interconvertibility of the zones of activity suggests that the compounds concerned are closely related chemically and exist on the paper in a state of equilibrium with each other.

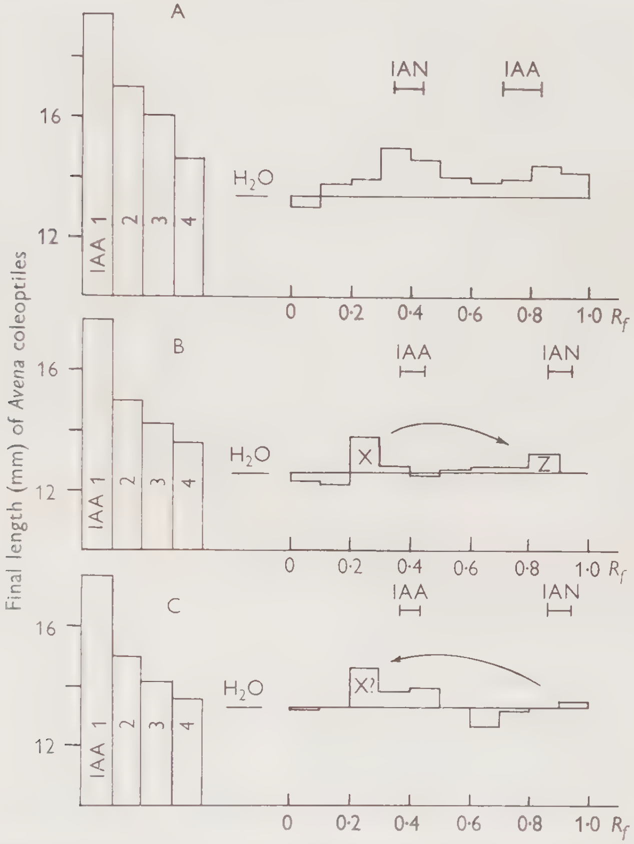

Fig. 2. Interchangeability of zones on chromatograms of marine phytoplankton. A, zone R_f 0·8–1·0 of Fig. 1 A eluted and re-chromatographed in water. B, zone R_f 0·2–0·6 of Fig. 1 C eluted and re-chromatographed in *iso*-propanol-ammonia. C, zone R_f 0·6–1·0 of Fig. 1 F eluted and re-chromatographed in *iso*-propanol-ammonia. IAA controls are as in Fig. 1.

The interconvertibility of X and Z may be related to a similar phenomenon observed in extracts of tomato roots, in which three compounds, X, Y, and Z, were shown to be mutually interconvertible (Britton *et al.*, 1956). The same phenomenon is also reported in extracts of pea roots (Audus & Gunning, 1958), and in various pure algal cultures (Bentley, 1958*a*). There is evidence on several of the algal chromatograms of the existence of zone Y, though this is only transient. This may be because chromatography in the present work was usually in ammoniacal *iso*-propanol. It was shown in work on tomato roots that X and Y may not be separated in this solvent mixture, whereas they are easily separated in ammoniacal butanol. Zone X in tomato, when separated from zone Y, usually ran behind IAA: this has been noted in the present work also. If the tomato and pea auxins are in fact the same as the algal hormones, we are obviously dealing with substances of wide distribution in the plant kingdom and probably of importance in fundamental cell metabolism. It is clearly important that their chemical constitutions should be investigated further. The interconversions demonstrated between X, Y, and Z suggest that the compounds are probably closely related chemically.

A shifting of the zones of activity has also been observed in the neutral fraction (Fig. 2 C), in which an active zone near the solvent front has been eluted and re-chromatographed in *iso*-propanol-ammonia. A new zone of activity appears near the starting line. Not enough information is as yet available on the neutral fraction to say whether this means that the same compounds are involved as in the acidic fractions.

Marine zooplankton

Extracts of marine zooplankton also showed activity, but of a rather different pattern from the phytoplankton samples (Fig. 3). Very little activity could be located in the EA fraction. Fig. 3 A represents the highest activity obtained, and usually chromatograms were negative. Considerable activity, however, was obtained in the SA fraction (Fig. 3 B), in the same position as the EA fraction. Surprisingly, the same zone of high activity was also located in the SN fraction (Fig. 3 C). When the SN fraction was run in *iso*-propanol-water, without ammonia, the activity was located at the solvent front, suggesting that it may be due to an acidic compound. The EN fraction contained no activity.

The EA and SA fractions of zooplankton sample II gave very much the same results as sample I, with a zone of activity running in the IAA position and a positive Ehrlich reaction, indicating an indole compound, at around R_f 6·0. The high activity detected in the SN fraction of sample I was not found in sample II.

Sea water

Fig 4 A shows the results of bio-assay of a chromatogram of the ether fraction of the offshore sample, run in *iso*-propanol-ammonia. There are two clear-cut zones of activity corresponding to zones X and Z located in the

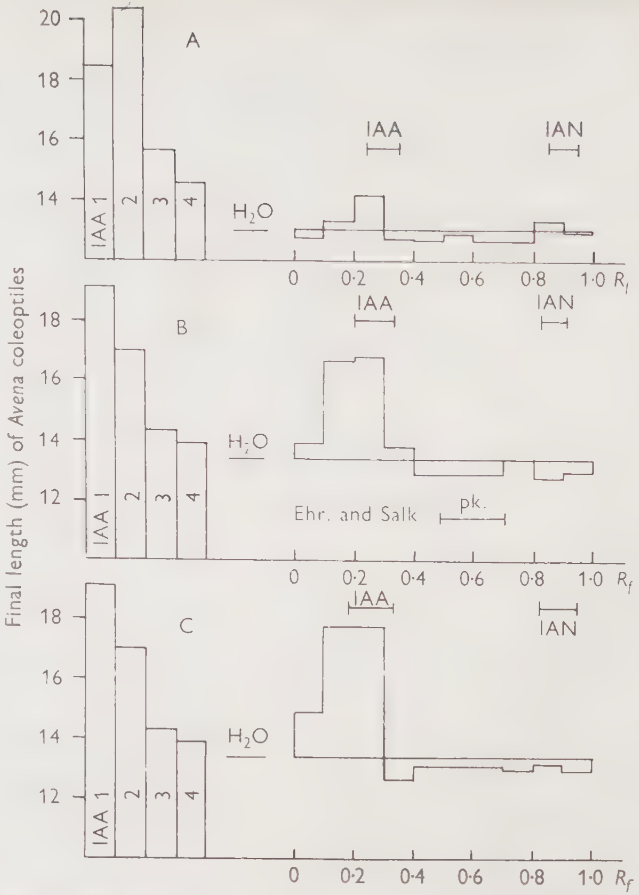

Fig. 3. Extracts of marine zooplankton chromatographed in *iso*-propanol-ammonia. A, EA fraction of sample I; B, SA fraction of sample I; C, SN fraction of sample I. IAA controls are as in Fig. 1.

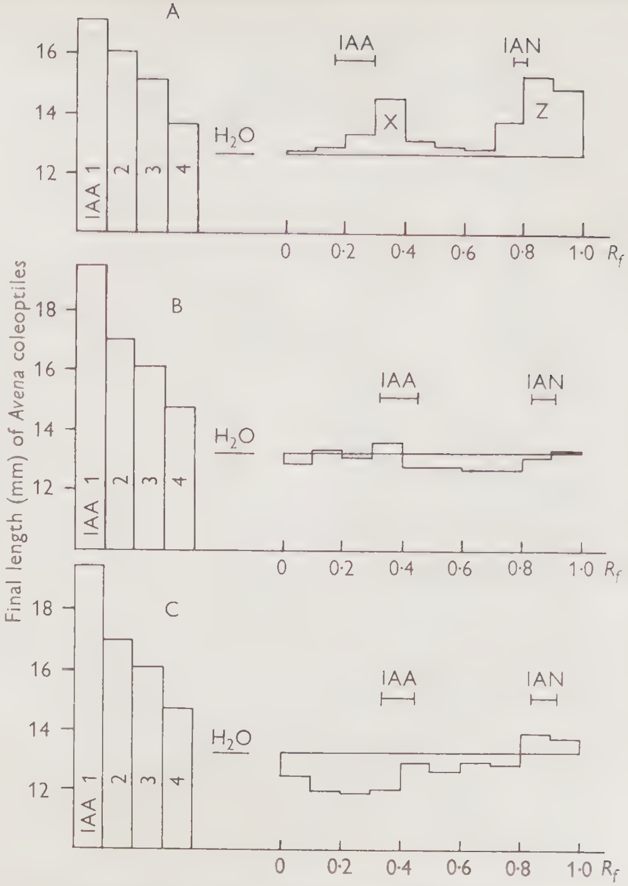

Fig. 4. Extracts of sea water chromatographed in *iso*-propanol-ammonia. A, Ether fraction of sample I; B, EA fraction of sample II; C, EN fraction of sample II. IAA controls are as in Fig. 1.

phytoplankton extracts. No colours were obtained with the Ehrlich or ninhydrin reactions.

A further extraction of 200 l. of inshore sea water was then carried out. The acidic ether fraction (Fig. 4 B) showed only slight promotion, not significant, at the positions of X and Z on chromatography in *iso*-propanol-ammonia. There was slight inhibition from R_f 0·4–0·8 corresponding to the β-inhibitor zone frequently reported in higher plants. The results rather suggest that the inhibitor is interfering with activity in the X and Z zones. The neutral ether fraction also showed considerable inhibition nearer the starting line, and slight promotion at position Z (Fig. 4 C). No Ehrlich colour reaction was obtained with either fraction, although the EA fraction showed strong yellow or brown fluorescence along the whole length of the paper. Inshore sea water is likely to be much more highly polluted than offshore water, and the inhibiting zones may be due to toxic substances of no physiological significance. The aqueous ether-insoluble fraction of these sea-water samples was not examined, as special methods need to be developed to deal with the large quantities of salts present.

DISCUSSION

The foregoing results establish that marine phytoplankton contains biologically active substances with activity similar to the auxins of the higher plants. Auxin activity has also been located in zooplankton samples, and in sea water. The main bulk of the activity in the acidic fractions of the phytoplankton and sea water is located in two zones, which have been called zones X and Z, although these zones do not necessarily represent the same substance in all the species examined. Zone X runs usually at an R_f of approximately 0·3–0·5, and Z at R_f approximately 0·9, in ammoniacal *iso*-propanol. The activity in the saponified fractions indicates that there are water-soluble, ether-insoluble auxin precursors in the algae. These ether-insoluble compounds yield ether-soluble auxins on treatment with alkali. It is possible that the active compounds located in the saponified fractions are the same substances as the ether-soluble auxins present in the materials originally (the EA fractions), as both sets show a similar mutual inter-convertibility. It is suggested that X and Z may be released to a limited extent from an unstable water-soluble complex by manipulative treatments during the extraction, and so would be found in the acidic ether fraction without any alkaline treatment.

The two major zones of activity located in the acidic fractions (X and Z) correspond to the positions of IAA and IAN on chromatography in ammoniacal *iso*-propanol, but neither IAA nor IAN gives activity other than in its own position on chromatograms when eluted and rechromatographed. The possibility that IAA and/or IAN are present in the extracts cannot be dismissed, since biological activity is obtained at the position of these compounds in both ammoniacal *iso*-propanol and water. One must conclude, however, that other compounds (referred to in this work as X and Z) are also present in these active zones, since they show a mutual inter-convertibility which is not shown by IAA and IAN.

The total amount of auxins (zones X and Z) located in the offshore sea water, calculated in terms of the IAA controls bio-assayed in the same experiment, is 0·375 μg in 110 l. (0·06 μg in zone X and 0·315 μg in zone Z). An improvement in the growth of a marine diatom, *Skeletonema costatum*, under the influence of IAA at a concentration of 10^{-11} to 10^{-10} g/ml. has been noted (Bentley, 1958*a*). This is equivalent to 1–10 μg in 100 l. Thus the amount of auxin detected in sea water is approximately ten times less than would be needed to have an optimum effect on the growth of *Skeletonema*. It should be borne in mind, however, that the amounts of auxin finally detected by bio-assay of extracts are probably much less than those present in the original materials due to losses in the many stages of purification and assay.

The investigations reported in this article have been carried out during the tenure of a Senior Government Research Fellowship, and I am indebted to the Director of the Department of Agriculture and Fisheries for Scotland Marine Laboratory for facilities for the work.

SUMMARY

Extracts of marine phytoplankton, marine zooplankton and sea water have been examined for plant hormones of the auxin type. The phytoplankton consisted predominantly of diatoms, in particular of *Leptocylindrus danicus*, *Chaetoceros debilis* and *C. decipiens*. The zooplankton consisted predominantly of copepods, in particular *Temora*, *Calanus* stages I–IV and *Para*/*Pseudocalanus*. The samples were extracted chemically and the extracts split into acidic and neutral components of (*a*) the ether-soluble fractions, and (*b*) the ether-soluble fractions of the residue after alkaline hydrolysis. The fractions were further purified by paper chromatography in water followed by chromatography in ammoniacal *iso*-propanol. They were assayed for biological activity by the *Avena* straight-growth test, which measures the activity of auxins in cell-enlargement.

Biological activity was detected in all phytoplankton fractions. Activity in the acidic fractions is mainly due to two hormones, tentatively called X and Z. These are probably closely related chemically, as they show a mutual inter-convertibility. The same two zones of activity were detected in sea water. The zooplankton samples also contained active substances. Indole compounds can be detected in the extracts, but it is not clear that the biological activity is due to indolylacetic acid or any of the known indole hormones.

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THE LIGAMENT OF *COCHLODESMA PRAETENUE* (PULTENEY)

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(Text-fig. 1)

In a recent paper (Allen, 1958) the ligament of *Cochlodesma praetenue* (Pulteney) was shown to have unusual features, the significance of which was not appreciated at that time. Examination of its structure shows that a further description is necessary.

Studies by Owen, Trueman & Yonge (1953), Owen (1958, 1959), and Yonge (1953, 1957) have made clear the basic structure of the ligament of the adult bivalve. Primarily the ligament is composed of an inner layer covered by the anterior and posterior outer layers and the periostracum. The inner layer is secreted by the epithelium of the mantle isthmus, the outer layers are secreted by the outer surface of the outer mantle fold within the depths of the mantle embayments at either end of the mantle isthmus, and the periostracum is secreted by the inner surface of the outer mantle fold. This primary ligament may be secondarily extended anteriorly and or posteriorly by fusion of the mantle margins and may involve (1) extension by periostracum, or (2) extension by fusion layer.

The ligament of *C. praetenue*, although much modified, is opisthodetic, i.e. the point of minimal growth is anterior (Owen, 1959; Allen, 1960). The primary ligament is secondarily extended anteriorly and posteriorly by fused periostracum and fusion layer. These secondary layers can be seen externally and are remarkable for the unusual paired lateral extensions of the fusion layer which follow the line of the umbonal ridge (Fig. 1). The primary ligament is internal. The ligament is best described by analysis of its various parts.

The inner layer lies below the umbo. It is held between a pair of spoon-shaped extensions of the pronounced internal ridges of each shell valve (see Allen, 1958, fig. 2). The lateral faces of the inner layer attached to the spoon-shaped extensions are concave, while the free ventral edge is grooved in the sagittal plane. Growth lines show that most of the growth takes place ventrally and posteriorly (Fig. 1 C).

The posterior outer layer is applied to the postero-dorsal sides of the inner layer. It is wedge-shaped and all growth is posterior. The growth lines are continuous with those of the inner layer. The lateral faces are slightly convex.

The posterior fusion layer covers the dorsal side of the posterior outer layer and extends to a point close to the anterior limit of the posterior adductor muscle.

The anterior outer layer is remarkable for its scroll-like form. It extends a short distance anterior to the posterior outer layer and fans out forming a pair of lateral wings. From the posterior edge of the wings a thin sheet of this layer extends ventrally overlapping the inner layer to a slight extent (Fig. 1 B, C). This gives the erroneous impression that the anterior outer layer is merely a continuation of the inner layer (see Allen, 1958, p. 98).

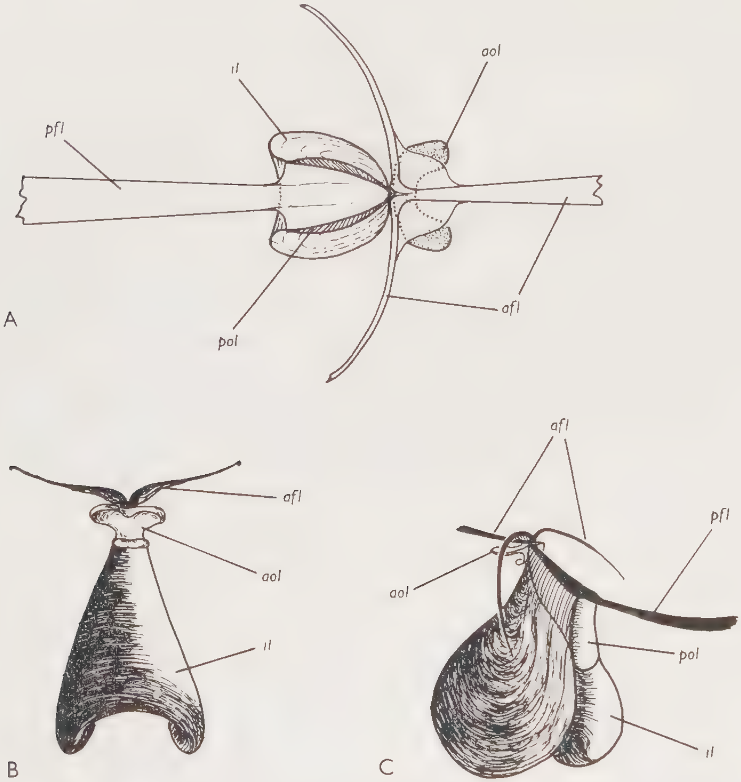

Fig. 1. Semi-diagrammatic views of the ligament of *Cochlodesma praetenue* as seen (A) dorsally, (B) anteriorly and (C) postero-laterally. *afl*, anterior fusion layer, *aol*, anterior outer layer, *il*, inner layer, *pfl*, posterior fusion layer, *pol*, posterior outer layer. The covering periostracum is not shown.

The anterior fusion layer is also unusual. It extends from just posterior to the anterior adductor muscle to the posterior limit of the anterior outer layer where it divides into two lateral forks that follow the line of the umbonal ridge. The angle between each fork and the sagittal part has a thin covering of fusion layer, which is separate from the underlying wings of the anterior outer layer (Fig. 1 A, B). A fold of epithelium extends between the two layers.

The fused periostracum covers the ligament and extends slightly beyond the anterior and posterior limits of the fusion layer.

It is clear that this ligament, although unusual, does not differ basically in its constitution from any other opisthodetic ligament. Posterior fusion layer, posterior outer layer and inner layer are normal. It is the lateral extensions of the anterior outer layer and anterior fusion layer that are atypical. It seems likely that these are formed by extension, lateral folding and fusion of the outer mantle edge in the depths of the anterior embayment.

SUMMARY

The ligament of *Cochlodesma praetenue* is described. Although unusual in form, it does not differ basically from other opisthodetic ligaments.

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ON CHANGES OF SEA TEMPERATURE IN THE ENGLISH CHANNEL

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(Text-figs. 1–5)

In a series of papers dealing with changes in the distribution of intertidal animals around Britain, and especially along the English Channel, attention was drawn to some local aspects of the general warming-up of sea and air that has taken place in the last 50 years (Southward & Crisp, 1954, 1956; Crisp and Southward, 1958). In the first of these papers smoothed values of annual mean air temperature at Plymouth Hoe, and sea surface temperature of the southern Celtic Sea were given, the latter values being based on Smed (1952). The graphs showed a rise of about 1° C in the air temperature and 0·5° C in sea temperature during 50 years.

More recently Cooper (1958) has tabulated the monthly mean sea temperatures for Plymouth Sound, based on three times a week readings taken below the Hoe by the Plymouth City Meteorologist. He interprets the figures as showing a rise of about 0·3° C, but does not give the annual means for the whole period. Annual means may not illustrate fully the effect of a very cold spring and very hot summer in the same year (e.g. 1947) but they do allow rapid comparison for biological purposes, and have considerable significance when resident or sedentary perennial species are being studied, whether they are pilchards or barnacles, for example.

In view of the increases in temperature already noted it would be surprising if a similar rise was not found at International Station E1, which has been worked, with some gaps, since 1903. Some monthly values for this station were given by Atkins & Jenkins (1952), but they showed no long-term trend. The apparent absence of any change may well have been due to the use of the integral mean of the whole water column; a dubious procedure for temperature. However, Cooper (1958), after remarking that he himself had failed to find any evidence of long-term changes at E_1, points out that there are inevitably many sources of bias in the raw data, which requires tedious treatment to make it statistically reasonable. Such treatment may be possible in the future (Cooper, personal communications), but there is an immediate need for information of use in current investigations of bottom fauna, plankton and other fields. Therefore, I have reassessed part of the E1 data, using only the observations of most interest—surface values, for comparison with the many surface observations in other areas, and bottom values for use with studies of bottom fauna and deeper living plankton animals.

Most of the actual observations at E1 have been published by the International Council, those for the period 1921–30 in the Rapport Atlantique, and those for 1931–38 and 1947–54 in the Bulletin Hydrographique. I am indebted to the observers, Mr F. A. J. Armstrong and Mr E. I. Butler, for the later observations which have not yet been published. For each year the temperatures observed each month have been plotted on graph paper, and the points joined together with a slightly smoothed freehand curve (example in Fig. 1). From the curves the mid-monthly values were read off, and additional values provided for missing months. The monthly temperatures derived in this way are presented in Table 1.

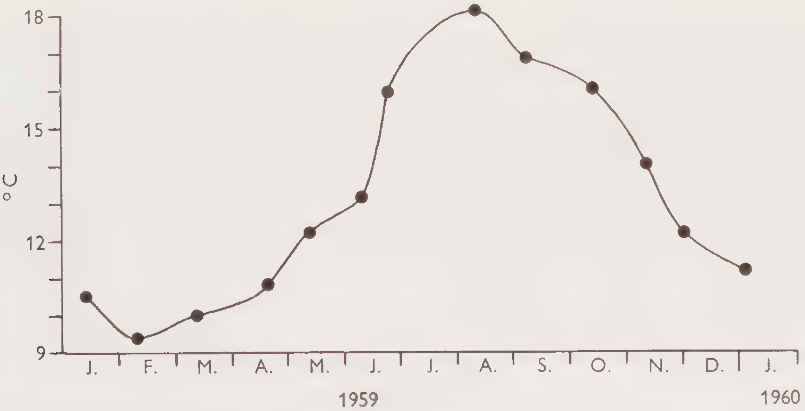

Fig. 1. An example of the method used to derive mid-monthly means from the raw data for E1. The points on the slightly smoothed curve are the actual surface temperatures observed in 1959.

Such treatment is only a little better than use of the raw data for calculating the annual means, and as a way of deriving the monthly values has been described by a colleague as 'fudging'. However, at the moment, it is difficult to find any other manipulation to make the E1 results more presentable, except, perhaps, comparison with other stations for surface values, and I believe that it is preferable to abandoning the whole series of observations.

SURFACE TEMPERATURE AT E1

In addition to Table 1, the annual means of surface temperature are plotted in Fig. 2, which also shows the annual means for 1903–27 worked out by Lumby (1935). Lumby's method involved adjustment to make up for missing months, and there is good agreement for all but one of the overlapping years.

TABLE 1. DERIVED MID-MONTHLY VALUES OF SEA TEMPERATURE AT INTERNATIONAL STATION E1 (LONG. 50° 02′ N., LAT. 4° 22′ W.)

Surface temperatures (0–0·5 m. depth)

	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
Jan.	—	11·0	9·7	9 1	11·0	10·0	9·5	10·0	9·8	10·1	9·6	10·8	9·8	9·2	10·9	9·4
Feb.	—	9·6	9·4	8·4	9·9	9·4	9·4	9·5	8·8	9·2	9·2	10·3	9·3	8·3	9·9	9·1
Mar.	—	9·5	9·4	8·1	9·3	9·6	9·3	9·5	8·8	8·4	9·1	9·4	9·7	8·6	8·9	9·4
Apr.	—	10·6	9·9	8·3	9·6	10 2	10·4	10·0	8·9	9·3	9·6	9·1	10·2	9·6	9·6	10·0
May	12·6	12·4	10·7	10·5	10·8	10·9	12·1	12·4	11·8	11·1	10·9	11·0	10·7	11·1	11·7	12·5
June	15·0	13·8	12·4	13·5	13 8	13·4	13·2	13·4	14·8	15·2	13·9	14·4	12·4	13·4	14·1	13·7
July	15·9	13·0	16·5	15·9	16·1	17·1	15·6	17·0	17·2	15·4	15·8	17·7	14·7	15·5	16·7	14·6
Aug.	16·2	15·0	16·7	15·1	15·5	17·1	16·8	16·0	16·5	15·2	15·2	17·7	18·7	15·6	18·2	16·5
Sept	15·8	14·9	14·9	14·2	15·7	16·9	15·4	16·9	17·0	16·4	15·0	15·6	16·8	15·2	16·2	15·9
Oct	15·5	14·0	13·0	12·9	13·7	14·8	13·8	14·3	13·1	14·1	14·8	13·7	15·3	13·6	13·8	14·7
Nov.	14·2	11·9	11·5	12·4	11·6	12·8	13·4	12·8	12·5	12·8	13·4	12·6	13·2	12·3	12·2	13·3
Dec.	12·6	10·6	10·0	11·7	10·6	11·2	11·8	11·3	11·2	11·4	11·9	11·4	9·9	12·3	10·4	11·6
Year	—	12·19	12·00	11·67	12·30	12·78	12·55	12·75	12·53	12·38	12·36	12·80	12·55	12·05	12·71	12·55

	1937	1938	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Jan.	10·0	10·2	9·4	11·1	10·7	10·8	9·6	10·3	9·6	10·9	9·8	11·0	10·3	9·9	10·3
Feb.	9·7	8·9	7·7	9·9	10·0	9·4	8·8	9·1	8·5	9·1	9·5	9·1	9·7	9·4	9·4
Mar.	9·6	9·1	7·9	9·1	10·3	10·1	8·7	9·1	8·5	9·2	7·7	8·6	10·4	8·9	10·0
Apr.	10·0	9·8	9·4	10·2	10·9	10·7	9·4	9·9	8·7	9·7	8·6	9·6	10·6	9·8	10·7
May	11·5	10·8	11·6	10·2	11·9	11·3	10 5	11·7	10·8	11·7	10·6	11·9	11·5	10·4	12·3
June	15·6	12·8	13·2	12·1	14·6	14·2	12·8	14·0	13·2	14·5	13·1	14·0	14·2	13·6	13·7
July	16·2	15·6	16·8	15·8	16·6	15·7	16·4	15·9	14·9	13·3	18·5	15·5	16·1	16·4	17·5
Aug.	17·8	17·7	17·6	17·0	15·8	15·8	15·4	15·9	17·4	14·2	16·0	15·2	16·0	15·7	18·0
Sept.	16·3	15·6	16·3	15·8	17·4	15·0	14·6	15·0	16·0	14·9	14·8	15·0	14·8	14·8	16·6
Oct.	14·8	14·0	15·0	14·3	15·5	14·2	14·0	13·7	14·5	13·7	14·1	14·4	14·8	14·4	15·9
Nov.	13·3	13·0	13·7	13·7	13·3	12·7	12·9	12·4	13·0	13·0	13·1	12·9	12·7	13·7	13·7
Dec.	11·6	12·7	12·4	12·4	11·7	10·9	11·7	10·9	12·7	11·0	12·1	11·5	11·3	12·3	11·5
Year	13·03	12·51	12·58	12·63	13·22	12·56	12·06	12·32	12·31	12·10	12·32	12·39	12·70	12·41	13·30

'Bottom' temperatures (60–75 m. depth)

	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
Jan.	—	11·2	10·0	9·3	10·9	9·7	10·6	9·8	9·9	10·3	10·1	10·9	10·1	9·4	10·3	9·6
Feb.	—	10·0	9·4	8·8	10·0	9·3	9·3	9·2	8·9	9·1	9·1	9·9	9·3	8·3	9·6	9·1
Mar.	—	9·6	9·1	8·4	9·1	9·4	8·9	9·6	8·5	8·3	8·7	9·6	9·1	8·2	8·9	9·0
Apr.	—	9·7	9·6	8·4	9·3	9·7	9·4	9·8	8·9	8·9	9·2	8·7	9·5	8·7	9·1	9·1
May	10·4	10·0	10·3	9·4	10·0	10·5	10·1	10·3	9·7	9·5	9·9	9·3	10·4	9·5	9·9	9·7
June	11·7	10·6	11·0	10·3	10·3	11·1	11·0	11·2	10·7	10·8	11·6	10·1	11·1	10·6	10·6	10·5
July	12·8	12·1	11·9	11·2	11·9	11·9	11·8	12·0	12·1	11·2	13·4	10·8	11·8	11·7	11·5	11·1
Aug.	13·3	12·9	12·5	12·2	12·3	12·6	12·5	12·9	12·3	12·0	14·8	11·5	12·6	11·8	12·9	12·8
Sept.	13·8	14·0	13·3	12·6	13·3	13·3	13·5	13·3	12·9	13·3	14·9	13·0	13·9	12·3	14·0	14·1
Oct.	15·2	13·9	13·4	13·1	13·5	14·4	13·7	14·3	13·9	14·0	14·7	13·8	14·7	13·1	13·6	13·8
Nov.	14·6	11·7	11·8	12·7	12·8	12·9	13·1	12·8	12·7	12·7	13·5	12·5	13·3	12·3	13·1	12·6
Dec.	12·9	10·7	10·2	11·7	10·7	11·7	11 5	11·3	11·5	11·5	11·9	11·1	9·9	11·6	10·6	11·5
Year	—	11·36	11·04	10·67	11·17	11·37	11·28	11·37	11·00	10·96	11·81	10·93	11·30	10·62	11·17	11·07

	1937	1938	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Jan.	10·4	10·5	9·5	11·2	10·7	10·9	9·6	10·4	9·5	11·0	10·1	10·9	10·6	10·4	10·4
Feb.	9·5	8·9	7·7	9·8	10·1	9·5	8·7	9·1	8·6	9·0	9·6	9·2	10·0	9·4	9·4
Mar	9·1	9·0	7·6	8·7	9·9	9·9	8·6	9·2	8·3	8·9	7·6	8·5	10·0	9·0	9·9
Apr.	9·3	9·4	8·4	9 3	9·8	10·3	8·9	9·3	8·7	9·3	8·0	8·9	10·5	8·8	10·1
May	10·1	9·7	9·5	10·6	10 5	10·6	9·5	10·0	9·3	10·2	9·5	9·6	11·0	9·9	10·6
June	11·1	10·1	10·3	11·3	11·4	11·7	10·6	11·0	10·5	10·7	10·6	10·7	12·0	11·0	11·6
July	12·2	12·1	11·3	12·3	12·8	12·1	11·2	12·2	11·2	11 5	11·3	12·0	12·5	11·7	12·6
Aug.	13·2	13·0	12·7	13 1	13·5	13·0	12 1	12·6	12·2	12·0	13·1	12·6	13·1	12·5	13·5
Sept.	14·4	13·5	13·9	13·7	14·8	14 0	13·0	13·9	12·9	13 6	13·1	13·7	13·8	13·6	14·8
Oct.	14·4	13·4	13·7	14·3	15·4	14·1	13 5	13·7	14·3	13·8	14·0	14·1	14·6	14·4	15·3
Nov.	13·3	12·8	13·1	13·5	13·6	12 7	13·1	12·5	13·0	12·9	13·2	12·9	12·8	13·6	14·8
Dec.	11·9	12·0	12·4	12 4	11·6	10·9	11·7	10 8	12·5	11·6	12·2	11·8	11·7	12·3	11·7
Year	11·57	11·20	10·84	11 68	12·00	11·64	10·87	11·22	10·91	11·20	11·02	11·24	11·88	11·38	12·05

The general trend is obviously upwards. Compared with 1903–27, the period mean for 1928–59 is 0·46° C higher, an increase of the same order as that found further west in the Celtic Sea (see p. 449). A distinct interruption of the rise occurred in 1951–56: during this 'little cold spell' there was a slight return of the northern barnacle, *Balanus balanoides*, at many stations in south-west England and elsewhere (Southward & Crisp, 1956; and unpublished records). However, even in this period the annual means were as high as, or higher than, those of the warmest years of 1903–11. The upward trend is also displayed in the very warm years. The year 1921 was regarded as exceptionally warm for the time (Le Danois, 1923; Harvey, 1923), but since then we have had at least two warmer years, 1949 and 1959. Looking at the graph, one might say that 1921 was the first major sign of the warm spell that set in a few years later, and which appears to be continuing still.

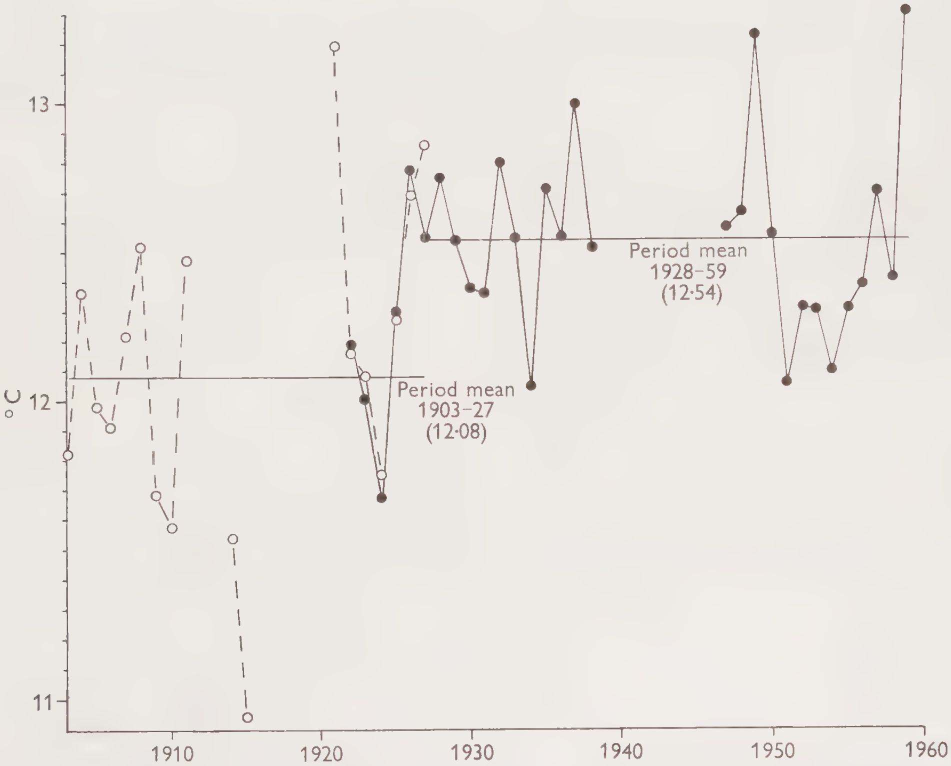

Fig. 2. Annual mean surface temperature at E1 1903–59. The black circles and solid lines are those from Table 1, while the open circles and broken line are the means calculated by Lumby (1935). Some period means are also shown.

If we examine the monthly values, the changes do not seem to have been quite so clear cut as with the annual means. The little cold spell mentioned above was marked by a sequence of cold winters (temperatures below 10° C from February to April), but in some of these years the summer was hot, which suggests a more continental, or less oceanic, marine climate than in earlier years. A similar trend since the late 1920's might be inferred from the monthly bottom temperatures also (Table 1). To contrast with this suggestion we have the generally warm years (e.g. 1949, 1959) when the surface temperatures in winter (Feb.–Apr.) were higher than the temperatures found in every year before 1939.

Probably the steadiest trend can be shown in the autumn months. There has been a slow rise in October, November and December, clearly demonstrated by grouping the figures into three periods:

	October (° C)		November (° C)		December (° C)	
	Mean	Minimum	Mean	Minimum	Mean	Minimum
1921–30	13·92	12·9	12·59	11·5	11·24	10·0
1931–38	14·33	13·6	12·91	12·2	11·45	9·9
1947–59	14·50	13·7	13·13	12·4	11·72	10·9

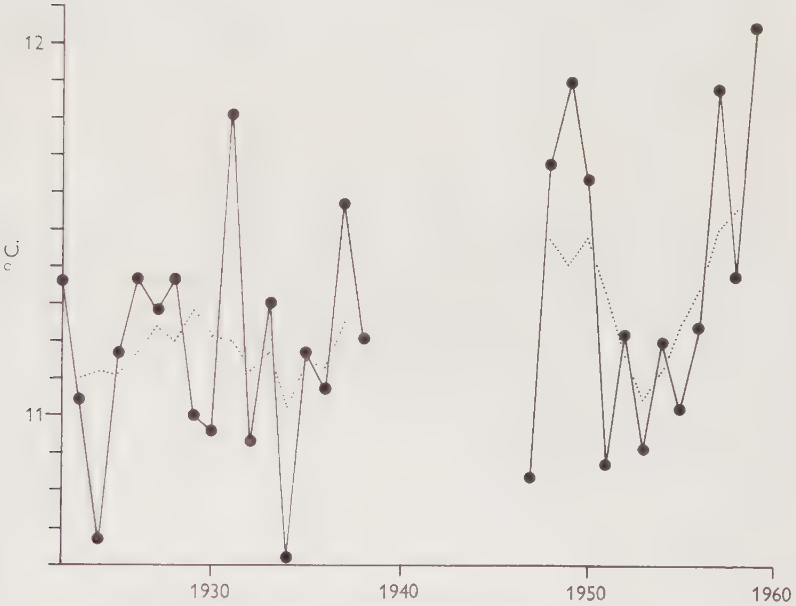

Fig. 3. Annual mean bottom temperature at E1, 1922–59. The dotted line shows the 5-year smoothed averages.

Thus there has been a rise of half a degree in the autumn means, and nearly twice this amount in the period minima. This autumn trend appears to be carried over into January, the monthly figures for which also show rises, but only about 0·2–0·3° C in this case. The cumulative effect of these increases on winter-spawning fish (the spring-spawners of Russell, 1935, 1939) can only be guessed at, but it is worth noting that Ford (1929) deduced a link between falling sea temperatures at E1 in the autumn and a successful herring fishery off Plymouth.

BOTTOM TEMPERATURE AT E1

From 1921 to 1959 the recorded depth of the lowest water sample at E1 has varied from 60 to 75 m. This is not, of course, due to variation in the sea-bed, but to combinations of inaccurate stationing of the ships, tide, wire angle and observers' idiosyncrasies. The derived monthly values for this 'bottom' are given in Table 1, and the annual means shown on Fig. 3, together with 5-year smoothed averages. The trends to be detected from the shorter period available are, of course, less marked compared with the surface. Nevertheless, the graph suggests part of a long-term rise, of the order of 0·25° C over 40 years. The monthly values, however, indicate that most of this rise has taken place in the autumn (Aug.–Jan.) and that the winter minima in March have become slightly lower. The annual range, for the period 1947–59, for example, is considerably wider than that of 1922–30.

THE YEARS 1921 AND 1931

The trends in surface and bottom temperatures do not always agree. In 1921 the bottom was relatively much warmer, compared with other years, than the surface, and the high temperatures recorded then were not exceeded until 1959. In the same way, 1931 was an unexceptional year at the surface but was another relatively warm year at the bottom: indeed, temperatures above 14° C persisted for a longer period than in 1921.

In considering the biological significance of these years with exceptionally warm bottom water, we have no evidence for the Channel in 1921, but that year in the North Sea the autumn and winter herring fisheries were very poor, and Le Danois (1923) has suggested a connexion. For 1931 there is much biological data to suggest the end of an epoch (Russell, 1935, 1939). It was the last year in which many plankton 'indicator' species were abundant or appeared off Plymouth, particularly the northern or boreal forms likely to be adversely influenced by warmer conditions—*Aglantha*, *Sagitta elegans*, and *Meganyctiphanes*, for example. To judge from the evidence obtained by Ford (to be found in Ford, 1933; Kemp, 1938) there was a practically total failure of recruitment of herring in the Plymouth area in the winter of 1931–32. This was not due to absence of adults, for considerable landings occurred, though 'running' herring were scarce (Ford, 1933). Herring are also northern forms and are likely to be adversely affected, not necessarily directly, by warmer conditions (cf. Russell, 1939). A thorough study of the recorded hydrographical conditions in the second half of 1931, in relation to the biological changes, would be very rewarding.

COMPARISON WITH OTHER REGIONS OF THE CHANNEL

Bowden (1955) has tabulated some annual means and period monthly means of the surface temperatures taken at the Seven Stones Light Vessel, and has shown graphically the annual means for the English Channel as a whole from 1903 to 1951. Mr A. J. Lee of the Fisheries Laboratory, Lowestoft, has kindly supplied me with further annual means for the Seven Stones to 1959. He has also supplied additional annual means to 1951 for Lumby area 9, for which Lumby (1935) has already published the means from 1903 to 1927. The annual means for these two stations are shown in Figs. 4 and 5, and it is obvious that the trends already shown for E1 are closely paralleled. At the Seven Stones the rise over 50 years has been about 0·5° C, though the peak

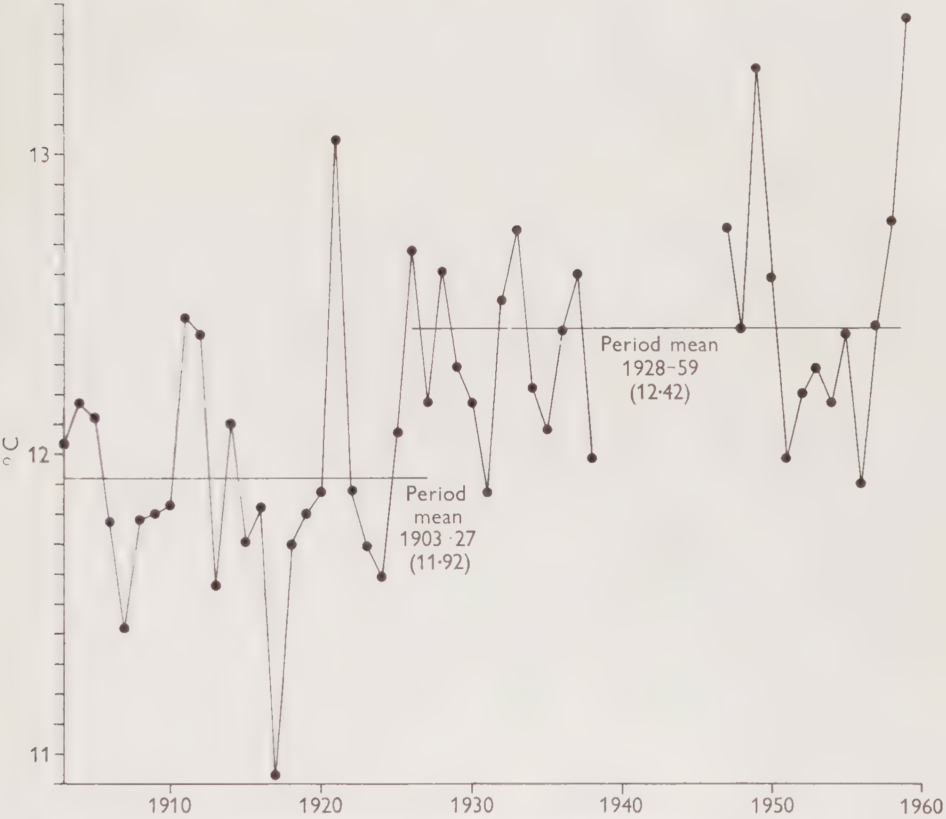

Fig. 4. Annual mean surface temperature at the Seven Stones Light Vessel, 1905–59. From Lumby (1935) and Bowden (1955), with means to 1959 supplied by Mr A. J. Lee.

in 1921 was less marked, and the little cold spell of 1951–56 relatively less cold than off Plymouth.

North of Ushant (area 9) the period means show a rise of 0·64° C, somewhat more than at E1 or the Seven Stones. A larger increase than elsewhere is not surprising if we remember that much of the warm water flow into the English Channel in summer (i.e. Aug.–Sept.) appears to be concentrated on the southern side (Lumby, 1925; Harvey, 1930; cf. also Dietrich, 1950). This area also shows a steadier trend than at the other two stations: it is not as coastal, and is less likely to be influenced by a flow of colder water in the winter (cf. Dietrich, 1950).

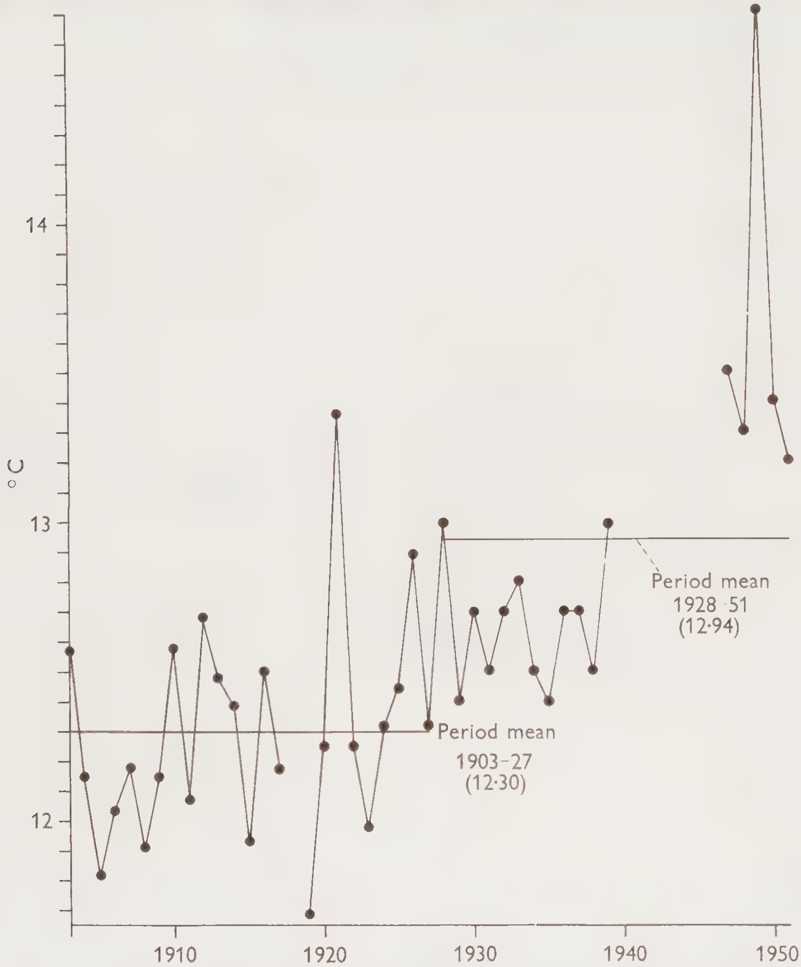

Fig. 5. Annual mean surface temperature in Lumby area 9 (area centred on long. 48° 40′ N., lat. 5° 20′ W.) north of Ushant (Ile d'Ouessant). From Lumby (1935) with additional means supplied by Mr A. J. Lee.

SUMMARY

Mid-monthly values of sea surface and bottom temperature, 1921–59, have been derived graphically from the raw data for International Station E1, and annual and other means calculated. The results are presented graphically and in tables, and discussed briefly in relation to faunistic and other changes in the English Channel.

Comparison with data from other areas suggests that in the Western Channel the annual mean surface temperature has risen about 0·5° C in the last 50 years. At station E1 the bottom temperature has also risen, about 0·25° C since the 1920's. The steadiest rise, in both surface and bottom temperatures, seems to have taken place in the autumn months.

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THE CILIARY FEEDING MECHANISM OF THE MEGATHYRIDAE (BRACHIOPODA), AND THE GROWTH STAGES OF THE LOPHOPHORE

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From the Plymouth Laboratory

(Text-figs. 1–11)

The Megathyridae Allan 1940 is a family of brachiopods in which the adult lophophore is of simple design, bilobed (schizolophous) in *Argyrotheca* and four-lobed (ptycholophous) in *Megathyris*. Little is known of feeding mechanisms in the family. Hérouard (1877), finding it difficult or impossible to observe the feeding currents of living brachiopods, constructed artificial lophophores of lead piping with fine perforations corresponding to the position of attachment of the filaments. Through these he forced water, while the artificial lophophores were immersed in a bowl of water. He assumed, wrongly, that the result would be similar to the action produced by cilia vibrating in water. His remarks on the working of an artificial lophophore resembling that of *Megathyris* (= *Argiope*) were transcribed by Morgan (1883) without making it clear that the observations were not his own and were not made on the living animal. Apart from Hérouard's work on artificial lophophores, the only reference to feeding in a member of the Megathyridae is that of Shipley (1883) who merely mentioned that in *Argyrotheca* the arrangement of the cilia is adapted to bring particles into the ciliated groove and thence to the mouth. Thus an examination of the method of feeding of the Megathyridae was considered desirable, and was made possible in the first instance through the kindness of M. Paul Bourgis, then, in 1955, on the staff of the Laboratoire Arago, Banyuls-sur-Mer. He sent two small consignments of living *Argyrotheca cordata* (Risso), *A. cuneata* (Risso) and *Megathyris detruncata* (Gmelin), received on the 28 October and 24 December 1955. They were taken on 'fonds coralligènes (construits par des Lithothamnides)', the first being dredged off Cap d'Aseille at a depth of 30–40 m, and the second from the Baie de Banyuls at a depth of 20–40 m. The successful method of sending these small brachiopods may be of interest. Each was rolled in damp filter-paper, and about a dozen packed in a little bag of thick polythene, which was then sealed and placed in a small (4 × 5 in.) flat case of a special kind of papier mâché. The case was enclosed in a tough envelope and sent by air mail. All the brachiopods arrived in good condition, although those received in December had been out of water for five days.

Further *Megathyris* were dredged by R. V. 'Sarsia' in May 1958 somewhat to the south-east of La Chapelle Bank (47° 25′ N., 6° 30′ W.) at a depth of 320–490 fathoms,[1] so that the exact depth is unknown, except that it was at least 320 fathoms. They were attached to the coral *Lophelia prolifera* (L.). These deep water *Megathyris* were of the transverse type. They did not attain the maximum size of those from Banyuls, the largest being 3·2 mm long and 4·6 mm wide, but they appear to be the same species, the only recent one of the genus. From these the growth stages have been worked out.

The Megathyridae withstand laboratory conditions well. Two *Megathyris* received from Banyuls in December 1955 lived until some time in 1958, when they disappeared after the entry of a crab from an adjoining tank. Specimens collected by R.V. 'Sarsia' in May 1958 lived in the tanks to April 1960, but there is evidently not sufficient food for them in the circulating water, for one opened in March 1960 was in a starved condition with very short filaments. Most of the few *Argyrotheca* were used within a few weeks of their arrival. One *A. cordata*, however, lived for over 6 months, but was in a starved condition when opened; the filaments were short and had dark orange coloured tips.

All figures, except Fig. 8, have been drawn with the aid of a camera lucida.

THE ADULT LOPHOPHORE

In *Argyrotheca* the invagination of the schizolophous lophophore (Figs. 1, 2) is occupied by a triangular septum, with its apex just in front of the mouth. In the young the septum has the shape of an isosceles triangle; in the adult it rises gradually from the anterior margin of the valve to its apex, then drops steeply to the valve floor, with a slight concavity facing posteriorly. At a length and width of 3·6 mm—the largest seen—the septum of *A. cordata* was not connected by a ridge with the cardinalia, but was followed posteriorly by a slight groove, with a low rounded ridge on each side. It is apparently in larger specimens than those seen that it is continued as a ridge to the cardinalia, as described and figured by Davidson (1887). The crest of the septum is toothed in *A. cordata*, smooth in *A. cuneata*.

The lophophore is supported by descending branches of the loop, which in *A. cordata* was said by Davidson (1887, p. 132) to be 'two-lobed, attached to the base of the hinge-plate and again to the anterior extremity of the submarginal septum, and more or less confluent with the valve'. His largest specimen was 2½ lines long and 2 lines wide, that is about 5·3 by 4·2 mm. Schulgin (1885) figured, under the name *Argiope kowalevskii*, incomplete descending branches in an individual of which the size was not given. Shipley (1883) figured and described them as incomplete at a shell length and width of 3 mm. He stated 'although these plates do not form a continuous support in front, there are traces of them in the anterior border, in the form of small

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[1] Given previously (Atkins, 1959*a*) as 400–405 fathoms and since corrected.

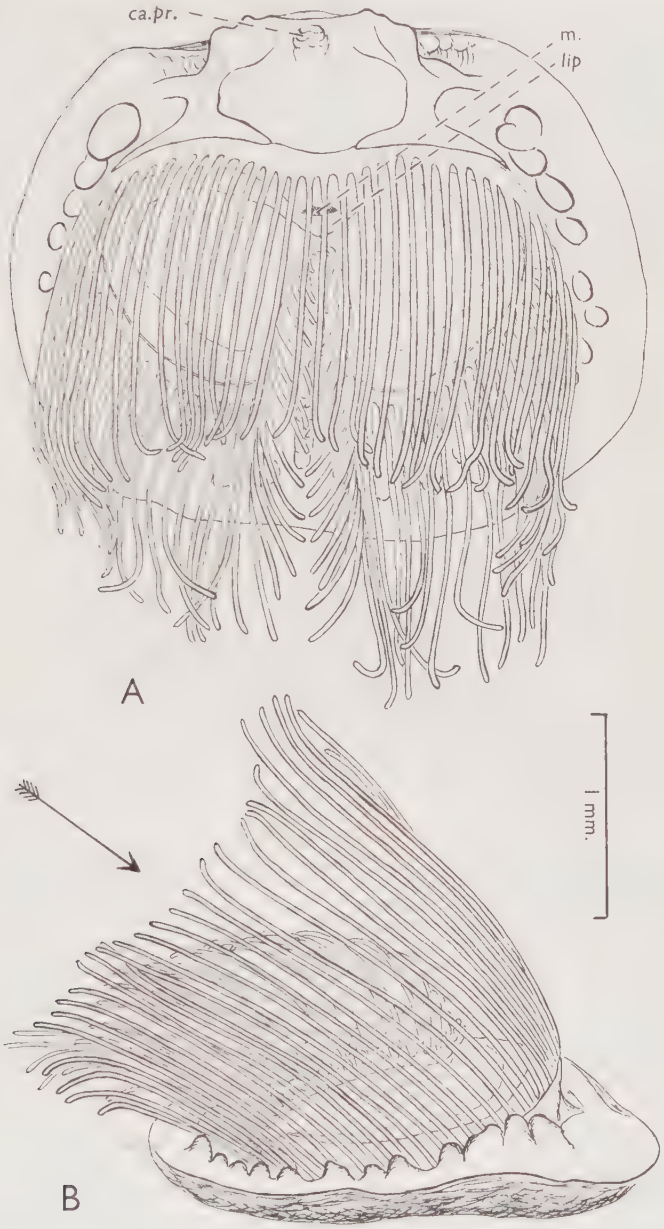

Fig. 1. *Argyrotheca cordata* of shell-length 3·0 mm and width 2·9 mm. Brachial valve with adult schizolophous lophophore, drawn living after narcotizing. A, ventral; and B, lateral view. *ca.pr.*, cardinal process; *lip*, lip of the food groove; *m.*, mouth. The arrow shows the direction of the inhalant current.

teeth'. These closely set 'teeth' actually lie well to the outside of the base of the lophophore as may be seen from Fig. 2 and as shown by Woodward (1880, fig. 161); the lateral and anterior ones might better be described as incipient submarginal septa. Posteriorly they buttress the descending branches of the loop. It may be that the full development of the loop occurs only in large specimens. In my largest *A. cordata*, of length and width 3·6 mm, the loop was only observable posteriorly and anteriorly, but in the position where the loop is figured by various authors a slight ribbon-shaped depression occurred, and here the shell mosaic differed superficially from that over the remainder of the valve in that the leaflets were radially orientated and more elongate. When present, the descending branches have the form of ribbons, which, except postero-laterally, are parallel with the valve floor, whereas in young stages of dallinids the ribbons are vertical to the valve floor (Atkins, 1959*b*).

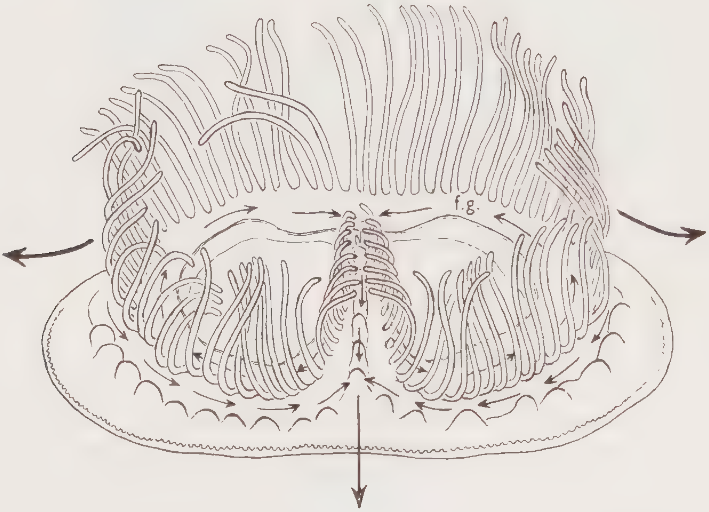

Fig. 2. *Argyrotheca cordata*. Anterior view of brachial valve, with lophophore somewhat contracted, of the same specimen as in Fig. 1. Large arrows indicate the main exhalant currents; small arrows the direction of a current on the mantle, between the lophophore and the submarginal tubercles, and also in the food groove (*f.g.*).

The loop was complete, although apparently confluent with the valve floor, in an *A. cuneata* of length and width 3·3 mm: this appears to be a good size for this species for Davidson (1887) gave the length as 1 line and width as 2 lines. Schulgin's (1885) measurements cannot be relied on as he confused the various dimensions of the brachiopod shell. It is to be noted that Blochmann (1910) described an incomplete loop in *A. australis* of length and width 3 mm.

Postero-laterally the descending branches of the loop support the lophophore as it passes from body to mantle. The filaments lining the sides of the median invagination are carried just below the anterior face of the septum, and as this runs at an angle to the valve floor, so does the line of filaments; the latest formed filaments arise near the apex of the septum, almost on a level with the mouth. By this arrangement the lophophore slopes both from the crest of the septum to the lateral mantle margins and from a high position posteriorly to the anterior mantle margin as shown by Shipley (1883, figs. 2, 3) and Schulgin (1885, figs. 15–18).

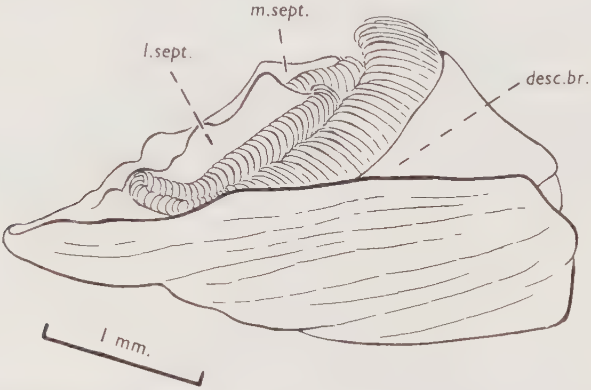

Fig. 3. *Megathyris detruncata* of shell length 4·8 mm and width 5·5 mm. Side view of brachial valve with ptycholophous lophophore strongly contracted, to show the postero-anterior slope of the lophophore. *desc.br.*, descending branch of the loop; *l.sept.*, lateral septum (right); *m. sept.*, median septum.

In *Megathyris detruncata* the adult lophophore is ptycholophous, there being a lateral invagination occupied by a septum on each side of the median septum. The lateral septa usually are not as high or as long as the median one, which has its apex just in front of the mouth. Occasionally five septa are present (Fischer & Oehlert, 1891, p. 104), but the additional two may be small and rudimentary, no doubt resembling the small submarginal septa of *Argyrotheca cordata*. The septa have sloping anterior faces, whilst posteriorly they drop steeply to the valve floor, with a slight backward-facing concavity; this was shown by Morgan (1883, figs. 6, 7). The crests of the septa are toothed. Morgan (1918) suggested that the schizolophe of *Argyrotheca* is derived from the ptycholophe of *Megathyris* by atrophy of the lateral septa. Thomson (1927, pp. 211–12) discussed this and concluded that the reverse was true, *Megathyris* passing through a schizolophous stage in its development. At the time he was writing the growth stages of the lophophore of *Megathyris* were unknown; the present work on them supports his conclusions. In the *Megathyris* examined, the descending branches of the loop could be clearly traced in some adults.

The filaments forming the sides of the invaginations arise just below the crests of the septa, and the brachial membrane, or floor of the lophophore, slopes to the frontal and lateral margins of the valves (figs. 3, 4).

On each side of the lophophore a small brachial canal, arising from a peri-oesophageal space, runs at the bases of the filaments and gives off a branch to each. In *Megathyris* a large brachial canal underlies the brachial membrane (Fig. 4, *b.c.g.*): this canal is most probably present in *Argyrotheca*, but in the small specimen sectioned, of length 2·6 mm and width 2·2 mm, it was most difficult to trace owing to collapse of its wall. In *Argyrotheca* the coelomic cavity, divided into two by mesentery and septum, underlies the lophophore to its anterior edge. In *Megathyris* the cavity is divided anteriorly into four by the three septa and these branches extend to the anterior extremities of the lobes of the lophophore (Fig. 4). Muscle fibres attached near the crests of the septa run under the great brachial canals.

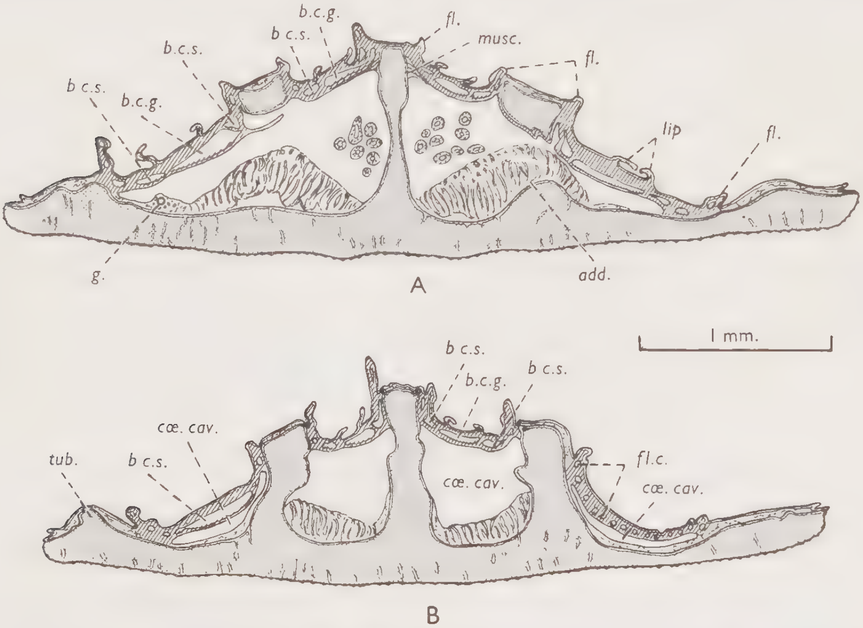

Fig. 4. *Megathyris detruncata*. Transverse sections of a specimen of shell length 3·8 mm and width 5·2 mm. A, through the posterior region of the lophophore, the backwardly projecting crests only of the lateral septa being cut; B, through the anterior region of the lophophore, near to the anterior ends of the lateral lobes. *add.*, adductor muscles; *b.c.g.*, great and *b.c.s.*, small brachial canals; *coe.cav.*, coelomic cavity; *fl.*, filament and filament base; *fl.c.*, filamentar canals; *g.*, gonad; *lip* of the food groove; *musc.*, muscle fibres; *tub.*, tubercle.

The section illustrated in Fig. 4B passes on the left anterior to the great brachial canal and on the right anterior to both small and great canals.

Shipley (1883, p. 507) described nerves passing to the lophophore; unfortunately the fixation of the specimens I sectioned was not good and the position and distribution of the nerves could not be determined.

In both *Argyrotheca* and *Megathyris* the filaments are all in a single series, an arrangement I have so far found only in these genera, but it probably occurs in *Lacazella* (= *Thecidea*) *mediterranea* (Risso), judging from the figure in Davidson's paper of 1852. It was noted by Dall (1871, p. 22) in *Argyrotheca lutea* (Dall) and both Shipley (1883) and Schulgin (1885) figured a single row in *Argyrotheca*: Thomson (1927) seems to have overlooked this fact. All the filaments have rounded or ridged frontal surfaces, resembling the inner filaments of other brachiopods (Atkins, 1958, fig. 13A). This arrangement and type of filament is possibly primitive, for in the brachiopods examined, including the inarticulate *Crania*, a certain number of the first formed filaments, which come to lie behind the mouth in the adult, are in a single series and are of the inner series type, although all other filaments are in a double alternating series of two types. The inarticulates *Lingula* and *Glottidia* differ in having all filaments in a double series.

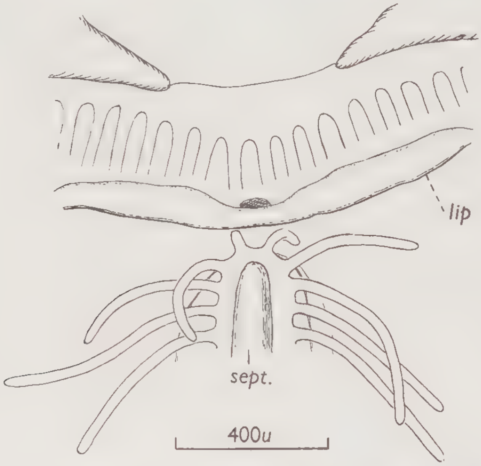

Fig. 5. *Argyrotheca cordata* of shell length and width 2·7 mm. To show the uninterrupted base of the lophophore and the uncrowded growth zone with two filament buds only. The filaments on the side of the septum are turned outward, as when the lophophore is partly contracted. This figure also shows the proximity of the mouth to the excurrent channel formed when the filaments bordering the septum are turned toward each other in the feeding animal. The lip of the food groove is turned outward. *lip*, edge of lip; *sept.*, septum.

Thomson (1927, p. 204) considered that the Megathyrinae Dall 1870 (= Megathyridae Allan 1940) were not ancestral to the Dallininae or Magellaniinae Beecher 1893 (= Terebratellinae Davidson 1886), but that *Megathyris* represents the highest development of a stock which branched off at an early stage of terebratellid development and was one of the two main divisions of the original terebratellid stock. The arrangement of the filaments in a single series supports Thomson's view.

In the Megathyridae the posterior and lateral filaments are long (Figs. 1 B and 7); they gradually decrease in length anteriorly and bordering the septa, the shortest occurring at the posterior edge of the median septum where new filaments arise. The base of the lophophore is continuous in the adult, as in the trocholophous stage, and filament buds are usually no more than two, of unequal length (Fig. 5). This is in contrast with the condition in those articulates with plectolophes or with spirolophes in the adult and in which the base of the lophophore becomes interrupted in the mid-line in the schizolophous stage and the two growth zones are crowded with young filaments and buds.

The food groove and its lip are wide in *Megathyris* and *Argyrotheca*. In an *A. cordata* of length 2·0 mm and width 2·2 mm the tightly coiled filaments were once seen to lie largely within the food groove, partly covered by the lip.

The supporting substance of the filaments in both genera is thick, especially basally, with a longitudinally fibrous appearance. In the living animal it shows shining white, except toward the tips of the filaments where it is attenuated.

The filamentar muscles are striated in both genera. This is of interest because the posterior adductor muscles—usually striated in articulates—appear to be unstriated in the Megathyridae (Dall, 1871; Shipley, 1883; Atkins, 1958)

THE CILIARY FEEDING MECHANISM

The following account of the ciliary feeding mechanism of the Megathyridae is based on an investigation of *Argyrotheca cordata*, *A. cuneata*, and *Megathyris detruncata*: the water currents were observed chiefly on *Megathyris* and proved exceptionally interesting because of the surprising reversal of the water currents, not so far seen in a brachiopod outside this family.

The Megathyridae were amongst the most difficult brachiopods studied; not only were they particularly sensitive to the slightest vibration, which caused them to close and remain closed for varying, but long periods, but after separation of the valves the filaments relaxed only slightly after 24 h, and attempts to relax them with 1% stovaine and with $7\frac{1}{2}\%$ magnesium chloride proved only partially successful: the latter was the more effective of the two.

Argyrotheca and *Megathyris* are attached by a short pedicle in a position almost at right angles to the substratum, and their beaks therefore suffer attrition. The valves gape to an angle of 40–45°, but this was only seen to occur after the animals had been in the laboratory tanks for some weeks. One *Argyrotheca cordata* extended the filaments well beyond the shell edge, as in Schulgin's (1885) figure 5. Observations on feeding were mostly made on *Megathyris* and most successfully on animals which had been in the tanks for 4 months, and when the temperature of the water was rising in April.

The position of the filaments during feeding was observed in a large *Megathyris*, about 6 mm long and 8 mm wide, which had been stood almost upright and was gaping widely so that the posterior ends of the three septa and the mouth could be seen. The filaments behind the mouth were erect except distally where they curved forward and touched on the anterior edge of the pedicle valve, extending beyond it slightly. The lateral filaments stood nearly erect, but slanting slightly forward, as did those at the anterior ends of the lobes—and curved slightly outward at their tips. The filaments on each side of a septum generally curved toward each other at their tips, but otherwise were nearly erect. Flocculent matter from the peridinian culture was seen to travel up the posterior filaments to their tips, where it remained. The tiny square-sided lappets edging the mantle lobes project at right angles to the valves. They probably interdigitate when the valves are closed, or nearly closed.

The ciliation of the lophophore

The single series of filaments have ciliated cells in three tracts, frontal and paired lateral.

The frontal cilia are long, about 20 μ, and, as in other brachiopods examined (Atkins, 1956, 1958, 1959*a*, *b*, *c*), are capable of reversal, beating either toward the base or toward the tip according to the quantity and size of particles impinging on the frontal surfaces of the filaments. In *Phoronis* also similar reversal of the frontal currents has been observed (Atkins, unpublished).

The lateral cilia, about 30 μ long, beat across the length of the filaments and have a well-marked dexioplectic metachronal wave. The lateral cilia, as well as the frontal, are able to reverse their beat (seen in *Megathyris*).

Abfrontal cilia could not be distinguished living and no abfrontal current could be detected: the abfrontal surface of the filament is small.

Shipley (1883, pl. 39, fig. 13) figured the cilia on the lateral and frontal surfaces of the filaments as all of the same length, while Schulgin (1885, pl. 9, fig. 26) showed the frontal cilia longer than the lateral, whereas the reverse occurs.

The brachial membrane is ciliated as shown by the movement of particles adhering to the tips of cilia: such currents as were observed passed toward and over the lip and into the food groove present at the bases of the filaments. The groove is interrupted near the posterior edge of the median septum, that is at the growth zone, and particles entering the groove on each side of it pass in opposite directions to the mouth. It is evident that on one side of a lobe the current in the groove is anteriorly directed and on the opposite side posteriorly directed (Fig. 8). The mouth, a large transverse slit, opens, as is usual, within the food groove in the mid-line posteriorly.

The ciliation of the mantle

In both species of *Argyrotheca* the mantle is ciliated: this is evident from the occasional movement of particles adhering to cilia, but although the animals were in good condition clear currents could rarely be demonstrated. On the posterior region of the pedicle valve a general anterior movement of particles was observed, as also along the crest of the median septum. The lophophore occupies much of the brachial valve: over the posterior region of the valve currents passed anteriorly and laterally. In *A. cordata* at the bases of the filaments, a broad current, between them and the submarginal tubercles, passed anteriorly and medianly and swept upward on to the median septum, joining the anteriorly directed current along its ventral edge (Fig. 2). This latter current is on the floor of the excurrent channel. No currents could be demonstrated between the submarginal tubercles and the mantle edge, although it seems probable that such exist. Submarginal tubercles are absent in *A. cuneata*.

In *Megathyris*, as in *Argyrotheca*, mantle currents were most difficult to demonstrate, although the movement of particles adhering to the tips of cilia, is evidence that the mantle is ciliated. In one specimen, on the third day after separation of the valves, feeble currents on the pedicle valve passed anteriorly to the free edge of the mantle. As in *Argyrotheca* the great extent of brachial valve occupied by the lophophore leaves only a small area of mantle exposed, and currents were not observed, except for an anteriorly directed current along the crest of the median septum.

The water currents (Figs. 1, 2, 5–8)

In *Megathyris* with valves gaping naturally, unnarcotized, the broad inhalant current is median and as it closely approaches the lophophore is drawn into the four lobes (two in *Argyrotheca*); the main part of the current, however, appears to pass into the posterior region of the lophophore where the posterior and lateral filaments are particularly long and so play a major part in creating the current. The filaments bordering the three septa generally curve toward each other over the septa—this is especially apparent over the median septum—their tips approaching or interdigitating, thus forming three excurrent channels. The exhalant current escapes between the filaments, and is strongest at the postero-lateral angles of the shell where it is fed by currents passing between the long posterior filaments and which can only escape here. Three antero-dorsal exhalant currents pass from the three excurrent channels floored by the septa and bordered by filaments. In both genera the median dorsal excurrent channel has its origin in front of the mouth where the filaments are short (Fig. 5). It is possible that this channel may carry away material voided from the mouth, although this has not been seen to occur. On one occasion in *Argyrotheca* the lip in front of the mouth was

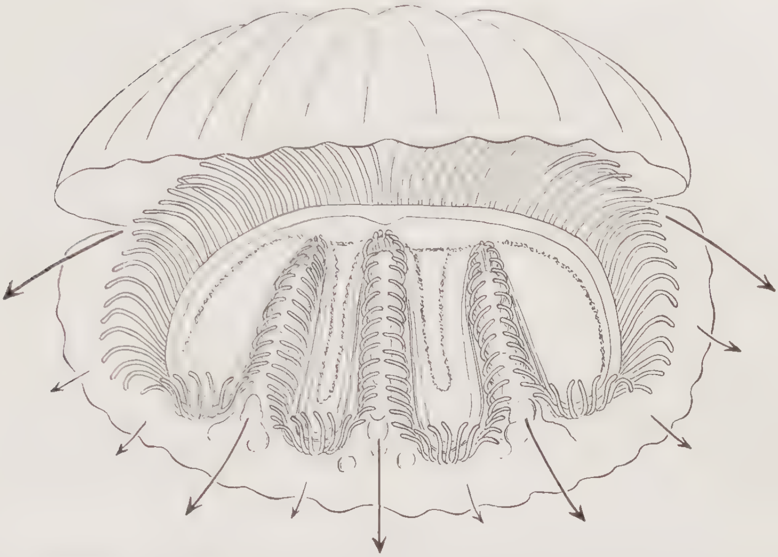

Fig. 6. *Megathyris detruncata,* View through the anterior gape of a feeding animal (unnarcotized), somewhat diagrammatic; filaments foreshortened. The exhalant currents only can be shown, for the inhalant currents enter the lophophore from the direction of the observer. Tracts of mucous glands on the brachial membrane are indicated.

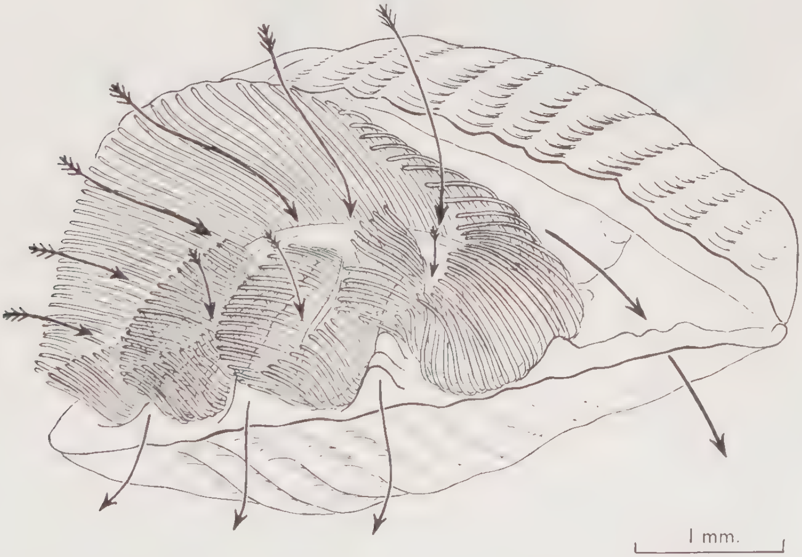

Fig. 7. *Megathyris detruncata.* Obliquely lateral view of a feeding animal to show the usual inhalant (feathered arrows) and exhalant (plain arrows) currents. Currents are reversed when strong cleansing action is needed.

turned outwards and the current on its inner surface, instead of passing into the mouth, passed away from it toward the excurrent channel, so evidently ciliary reversal occurs here.

In April 1956 momentary reversal of the water currents was observed a number of times in *Megathyris* gaping naturally and fed on peridinians and Aquadag. The usual inhalant and exhalant currents continued for some 5 min, then, without an interval, a total reversal of all water currents occurred and continued for 3–10 sec. At the end of this period of reversal no currents were detectable for 1–2 sec. Normal currents were then resumed. Reversal of the water currents was first noticed in a *Megathyris* viewed laterally, in which it occurred successively more than a dozen times. Particularly noticeable were the numerous peridinians in the reversed current leaving from the posterior region of the lophophore. On the following day the same animal was viewed from in front: it could then be seen that peridinians collected in the food groove across the entire posterior width of the lophophore. It is mainly peridinians from the groove which pass out from this region in the reversed current and their accumulation in the groove is doubtless one of the stimuli which sets off the reversal. The peridinians passing out were separate and not bound together by mucus.

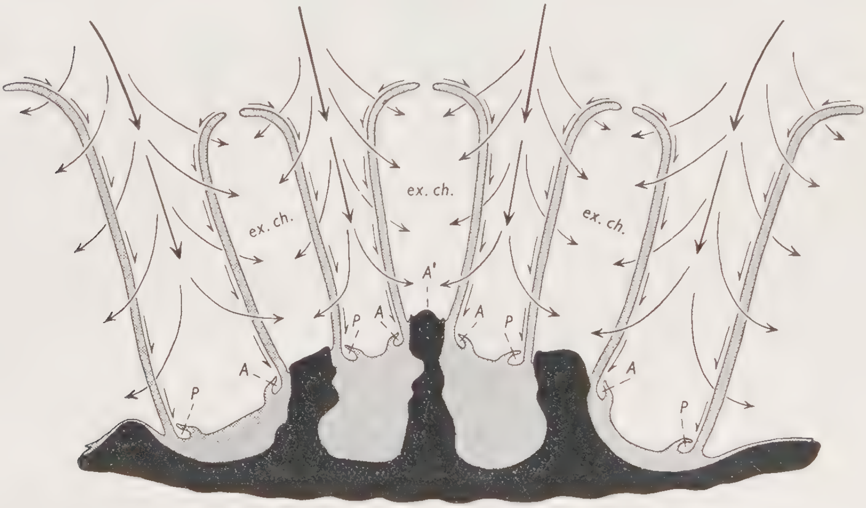

Fig. 8. *Megathyris detruncata.* Diagram (not intended to be proportionally exact) of a section through the lobes of the ptycholophous lophophore to show the direction of the inhalant currents and of the frontal currents on the filaments in the feeding animal. The direction of the currents is reversed when strong cleansing action is needed. A, anteriorly and P, posteriorly directed currents in the food grooves. A^1, anteriorly directed current along the crest of the median septum. *ex.ch.*, excurrent channel. The shell with the septa shown black.

The reversed water current is almost certainly due to reversal of the beat of the lateral cilia, although this could not be seen owing to the opacity of the valves and the low magnification which had to be used, nor could the metachronal wave be seen which might have given some indication of change of direction of beat. The valves were gaping widely, as in Figs. 6 and 7, and no movement of them or of the lips of the food groove could be detected, in fact no muscular movement whatever could be detected which might account for the reversal. On the third day the same animal, still in front view with valves gaping widely, but now with the filaments curved inwards and no water current detectable, suddenly showed slight reversed current.

Another *Megathyris* with valves gaping, but with filaments curved inwards at about half their length, showed no water currents or frontal currents on the filaments. A little Aquadag in sea water was dropped on to the lophophore and fell mostly into the two inner lobes. With the filaments still curved inwards, the reversed current began, and this apparently before any material had reached the mouth region. In this instance also a careful watch revealed no muscular movements.

On all occasions the reversed current was a steady continuous stream for the short while it lasted, and, judging from the movement of particles, quite as strong as the usual current. It would not appear possible that the frontal cilia beating toward the tips of the filaments could produce so strong a current, although *Megathyris* is a small animal: moreover, reversal of the water current seems to be set off by the collection of particles in the food grooves, whereas reversal of the frontal currents is caused by material impinging on the frontal surfaces of the filaments. Evidently the direction of the water current is reversed when strong cleansing action is called for.

Many Aquadag particles and peridinians passed out between the filaments all around the lophophore, yet a surprising number of the latter accumulated in the food groove across the posterior region of the lophophore.

Slight transverse movement occurred of particles on to the crests of the lateral septa, whence they were removed by the water current. The median septum had an anteriorly directed current along its crest, but the lateral septa appeared to be without such a current.

The frontal currents on the filaments

The frontal cilia of the filaments as mentioned previously (p. 467) are able to reverse their beat. Small particles impinging on the frontal surfaces are carried basally into the food grooves and thence to the mouth. The reversed currents toward the tips of the filaments are rejection currents and are seen when large or too many small particles are supplied. From the tips of the filaments rejected material drops off into the exhalant current. The rejection currents on the frontal surfaces of the filaments can occur without reversal of the inhalant and exhalant currents.

THE BEHAVIOUR OF *ARGYROTHECA CORDATA* DURING THE ESCAPE OF LARVAE

It is known from the work of Senn (1934) that *Argyrotheca cordata* and *A. cuneata* are hermaphrodite. They have paired brood pouches in which the ova develop and from which the free-swimming larvae escape (Kovalevsky, 1874, 1883; Shipley, 1883; Schulgin, 1885; Plenk, 1913). Larvae of both species were seen during October to January while the adults lived in the tanks.

Two *A. cordata* were watched under a dissecting microscope whilst liberating larvae. They opened widely, kept the filaments tightly folded inwards and at intervals snapped the valves together. The larger specimen (shell length 2·9 mm and width 3·0 mm) was watched for ½ h, during which time eight larvae escaped at varying intervals. The anterior commissure of the shell was facing upwards and the posteriorly situated brood pouches were visible through the gape. Part of the left lobe of the lophophore was wanting: the filaments of the right lobe were kept folded inwards, the posterior filaments were at times extended. Five of the larvae left the parent rapidly, swimming from the brood pouches and keeping near the pedicle valve; they swam toward the light and the surface of the water. Of these, four came from the left and one from the right pouch. When the valves first gaped a larva was seen caught in the filaments of the right side; it failed to escape during the ½ h the animal was watched. The first two larvae from the left pouch swam out in quick succession; the third after a long interval and the fourth near the end of the period of watching. They all left the shell ventrally and laterally. A fifth left this brood pouch, but failed to escape before the valves closed indefinitely. The first larvae to leave the right brood pouch swam out and away rapidly. The second nosed about, finally passed to the left side, escaping near the hinge and dropping to the bottom of the dish. The third behaved in the same manner, but was three times caught by the edges of the valve closing on it, the anterior lobe being outside. Finally, snapping of the valves shot it outside. On examination it appeared that this treatment had done it little harm. A fourth on leaving the brood pouch nosed about and was eventually shot out of the shell by closing of the valves. Judging by their behaviour these larvae were either unhealthy or had escaped prematurely. It is probable that larvae normally leave the parent rapidly, and during their escape the filaments are kept folded inwards so as not to interfere with their movements.

Larvae escaping naturally from these and other *A. cordata* in November 1955 lived some 10 days, but failed to attach themselves to the glass of the dish. Shipley (1883, pl. 40, figs. 28, 29) showed clearly the appearance of the ring of long and powerful swimming cilia when at rest and distinguished between them and the shorter, less active, cilia clothing the anterior lobe. He made certain observations on the behaviour of the free-swimming larvae.

THE IMMATURE SHELL OF *MEGATHYRIS DETRUNCATA*

Certain immature shells of *Megathyris detruncata* are figured (Figs. 9B, C, D and 10) to show the change in shape with age from elongate to transverse. The three smallest found were from Banyuls, attached near to or on adults. It cannot be altogether certain that these minute brachiopods, the largest 0·69 mm long, are *Megathyris*, for *Argyrotheca cordata* and *A. cuneata* were received at the same time, and all three megathyrids were probably dredged together. At this size it is doubtful if the three species could be distinguished with certainty. However, it is clear from the growth lines on the shell of the smallest *Megathyris*, length and width 0·97 mm, dredged by R.V. 'Sarsia' that when younger the shell was longer than wide. At a length of about 1 mm, width becomes greater than length and it is near this size that the first two rounded plicae are evident, with, between them a gentle indentation of the anterior shell edge (Fig. 10A, B); this becomes deeper with age (Fig. 10F). *Terebratalia transversa* (Sowerby), markedly transverse in the adult, is also elongate in the early stages (Atkins, 1959*c*), but this change in shape is of particular interest in the Megathyridae because of discussions by Jeffreys (1880), Davidson (1887), Fischer & Oehlert (1891) and Dall (1921) as to whether *Gwynia capsula* (Jeffreys) is an adult or an immature form of another species of megathyrid, such as *Argyrotheca cistellula* (Searles Wood) with which it is found. Thomson's (1927, p. 208) statement that it 'cannot be the young of that species from its more elongate form' is thus questionable. Jeffreys (1880), Davidson (1887) and Fischer & Oehlert (1891) were unable to find septum or loop in *Gwynia capsula* about 1·75 mm long and 1·3 mm wide. This is perhaps not altogether surprising as Jeffreys for one soaked the minute shells for several days in 'dilute potash water'. Such treatment is apt to cause disintegration of the shell in adult brachiopods before the flesh is sufficiently dissolved to brush or blow out of the shell. This is no doubt because organic matter enters into the shell substance. Dall (1921, p. 325), in the larger specimens he examined, found a distinct loop with its lower edge cemented to the valve, and thought the species sufficiently distinct though very near to *Argyrotheca cistellula*.

As *Megathyris* passes through a schizolophous stage at a shell length of 1–2 mm, where it is found together with *Argyrotheca* it may in some instances be somewhat difficult to distinguish between the two genera at that size, although *Megathyris* is likely to have greater width.

THE GROWTH STAGES OF THE LOPHOPHORE AND LOOP

Two minute brachiopods, 0·34 and 0·72 mm long were found attached to an adult *Argyrotheca cordata* and were possibly or probably the young of that species. In both the lophophore was completely circular. The smaller had

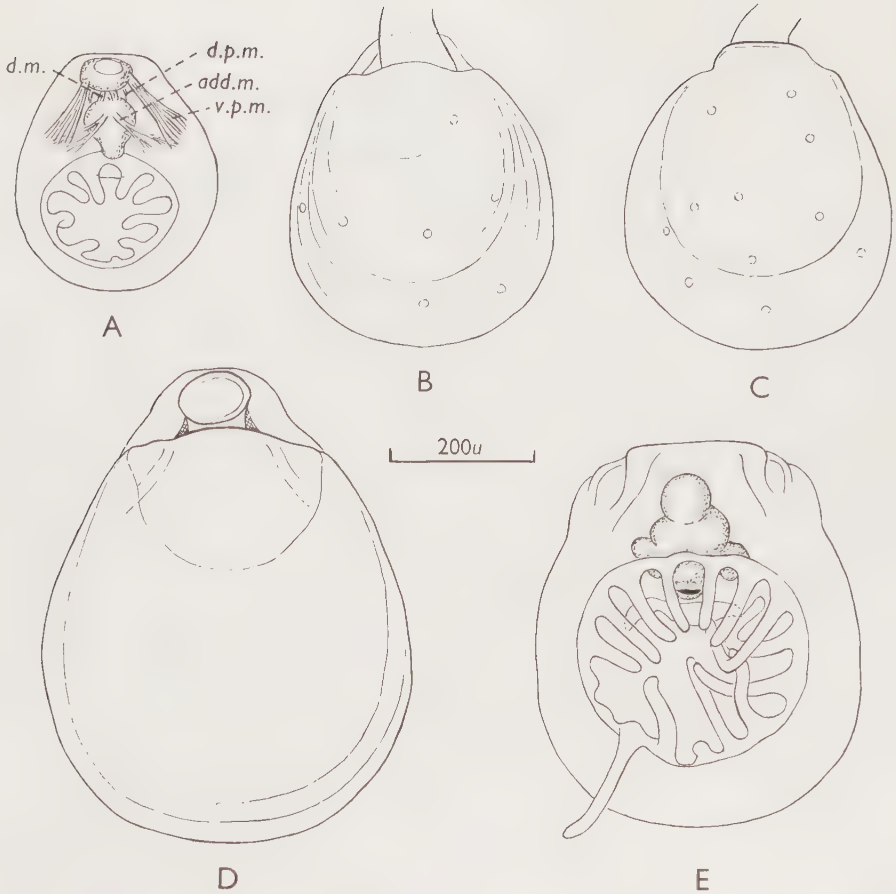

Fig. 9. A, *Argyrotheca cordata*: ventral view of a specimen of shell length 0·34 mm and width 0·29 mm, which was attached to an adult of that species; pedicle retracted. B–E, *Megathyris detruncata* from Banyuls-sur-Mer, two of which (B–D) were attached near to, and one (E) on an adult of that species. B, dorsal and C, ventral view of specimen of shell length 0·44 mm and width 0·38 mm; D, dorsal view of specimen of shell length 0·69 mm and width 0·52 mm; E, brachial valve with trocholophe of a specimen of shell length 0·62 and 0·46 mm. *add.m.*, adductor muscle; *d.m.*, diductor muscle; *d.p.m.*, dorsal and *v.p.m.*, ventral pedicle muscles.

four pairs of filaments and a bud; a small pre-oral lobe was present (Fig. 9A). Intestine and digestive diverticulata were as yet undifferentiated. This is a somewhat younger stage than that illustrated by Kovalevsky (1874) and reproduced by Oehlert & Deniker (1883) as their figure 11, for it has fewer filaments. Kovalevsky showed 10 filaments, but probably at least 12 were present, those behind the mouth being omitted, no doubt because they were obscured by the oesophagus and digestive diverticula. (In this figure the adductor muscles were apparently labelled diductors by Kovalevsky, although they are correctly identified in a figure of an older stage—Oehlert & Deniker 1883, fig. 13.) The larger specimen had nine pairs of filaments and a bud; the lobe in front of the mouth had extended laterally to about the base of the second or third filament on each side. Intestine and digestive diverticula were differentiated. This is about the same stage as that shown in Kovalevsky's figure reproduced by Oehlert & Deniker (1883) as their figure 13. In this figure only 14 filaments are shown, those behind the mouth—probably numbering four—again being omitted. I found no intermediate stages between these tiny individuals and the adult.

The growth stages of the lophophore of *Megathyris detruncata* have been worked out chiefly from material dredged by R.V. 'Sarsia', the youngest, however, were from Banyuls, attached near or on adults. The two attached near an adult *Megathyris* were 0·44 mm long and 0·38 mm wide (Fig. 9B, C) and 0·62 mm long and 0·46 mm wide. Although the smaller remained attached to the substratum, the tissue had deteriorated and the lophophore could not be distinguished: a few mantle pits were present. The lophophore of the larger was trocholophous, of the broad based terebratellacean type set low on the dorsal mantle, with eight pairs of filaments, the last on the right being a bud: two filaments on the left were abnormal (Fig. 9E). The lip of the food groove extended only a short distance on each side of the mouth. A third specimen 0·69 mm long and 0·52 mm wide (Fig. 9D) was attached to an adult *Megathyris*. It had a trocholophous lophophore with nine pairs of filaments: the lip of the food groove extended less than half way around the lophophore.

In the contracted condition the tips of the filaments were pointed inwards. When narcotized and expanded they extended upwards, outwards and forwards. Particles passed down the filaments and toward the mouth following the position of the food groove, although it was as yet unprovided with a complete lip. Reversal of the frontal cilia was not obtained on these tiny brachiopods because of the difficulty of dealing with them. The usual inhalant current would set into the circle of filaments and out between them, as described for the trocholophous stage of the lophophore in *Terebratulina retusa* by Atkins (1956).

The young *Megathyris* now to be described were dredged by R.V. 'Sarsia'. That shown in Fig. 10A–E had a length and width of 0·97 mm with the frontal edge of the shell slightly indented. The lophophore was damaged anteriorly, it was probably still trocholophous. Descending branches had grown from the crura (Fig. 10D). The dorsal septum was represented by a slight ridge in the mid-line. In the ventral valve a septum was present: the pedicle collar was fairly deep and had longitudinal pits (Fig. 10E).

A transverse individual of shell length 1·0 and 1·2 mm had a well-developed median septum and the lophophore, with about 14 pairs of filaments, slightly invaginated in the mid-anterior line. Descending branches from the crura had increased in length; their anterior ends could not be distinguished on the septum, but might have been hidden by filaments.

In a slightly larger, but less transverse individual, 1·2 mm long and 1·3 mm wide, the anterior invagination of the lophophore had deepened and

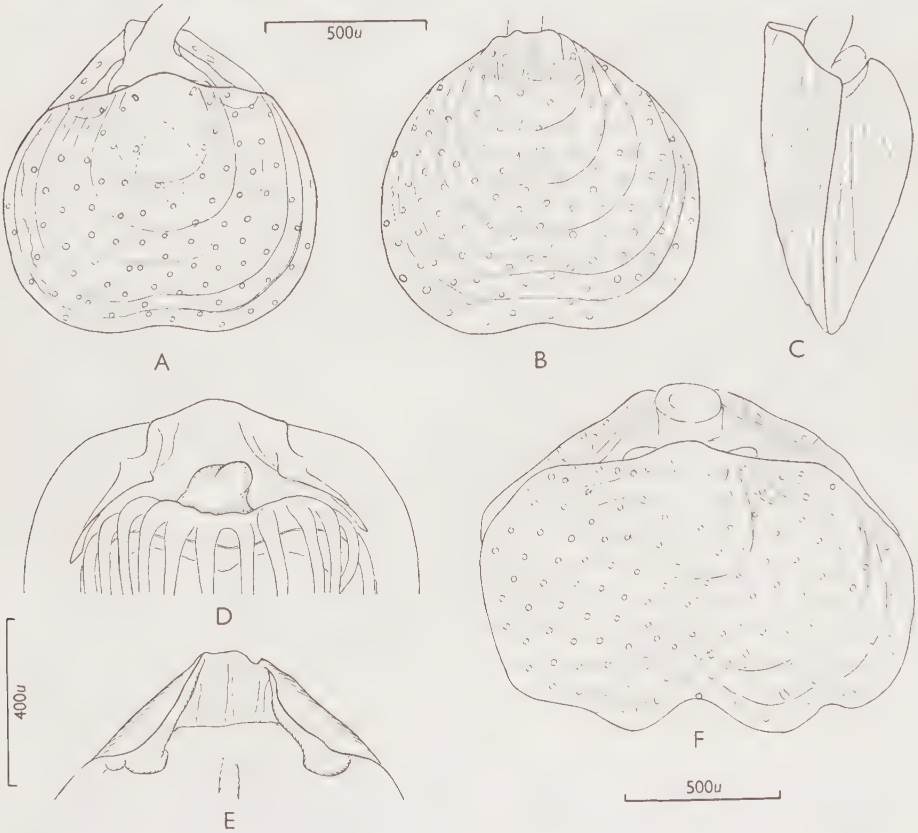

Fig. 10. *Megathyris detruncata* from near La Chapelle Bank, one (A–E) of shell length and width 0·97 mm and the other (F) of shell length 1·1 mm and width 1·4 mm. A, dorsal; B, ventral (ventral septum indicated by a broken line); C, lateral views; D, posterior region of the brachial valve to show the cardinalia and descending branches of the loop; E, umbonal region of pedicle valve to show the pedicle collar and the teeth; F, dorsal view with dorsal septum indicated by broken line.

descending branches had grown from near the ventral surface of the median septum (Fig. 11). The filaments in this individual were somewhat shorter than normal: it was possibly not entirely healthy, as it, and the previous specimen, had lived in the laboratory tanks for 16 months. These three individuals of length 0·97, 1·0 and 1·2 mm all had a gentle indentation of the anterior edge of the shell, due to the development of the first two plicae. Another two, of shell length 1·1 and 1·4 mm with early schizolophes, had in addition lateral indentations (Fig. 10F). The test of these small specimens was fairly thick.

At a shell length of 1·8 mm and width of 2·65 mm the lophophore was late schizolophous. No lateral septa were as yet present, and marginal tuberculation was absent. At length of 2·2 mm and width of 3·2 mm the lophophore was still in the same stage. Lateral septa were tiny and the lophophore only slightly indented, or rather flattened where these occurred. The margin had slight tuberculations postero-laterally. At a length of 2·4 mm and width of 2·7 mm the lateral septa were larger and the lophophore was ptycholophous.

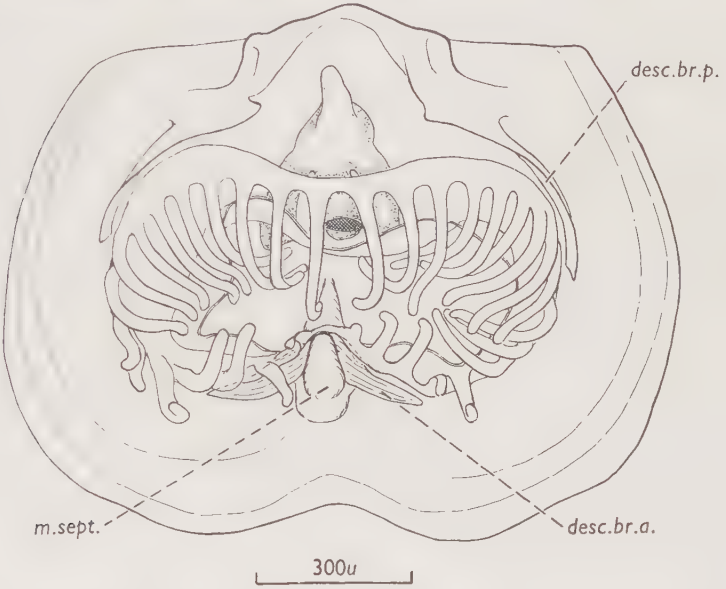

Fig. 11. *Megathyris detruncata* of shell length 1·2 mm and width 1·3 mm. Brachial valve with early schizolophe. The anterior ends of the descending branches (*desc.br.a.*) have grown from the median septum (*m.sept.*,) which alone is present. *desc.br.p.*, posterior end of descending branch of the loop. The filaments are shorter than normal. Drawn living, but not successfully relaxed.

Thomson's (1927, p. 214) description of the loop of *Megathyris* was as follows 'loop consisting of two descending branches which are free only near the crura, but descend (dorsally) to join the floor of the valve, rising over the two lateral septa, descending again to the floor of the valve, and attached to the sides of the median septum'. In *Argyrotheca* he described the descending branches as joining the anterior end of the median septum: according to him (p. 212) the loop-development of *Megathyris* had not then been clearly established. A loop which may disappear or be adherent to the valve floor in parts is puzzling, but I think it can be stated that in *Megathyris* the descending branches of the loop grow both from the crura and the median septum, and the junction of the two parts occurs in the region between the lateral septa and the crura. The anterior ends of the branches appear to arise at the crest of the median septum, in fact to overlie it, and run down its sides, with the anterior edges projecting as flanges all around the anterior face of the septum. This was seen at a shell length of 3·5 mm and width of 4·7 mm. *Megathyris* did not give good sections, owing to the large proportion of shelly matter, however, in the two individuals sectioned, it appeared that the descending branches were fused with the sides of the medium septum. Between the bases of the median and lateral septa the loop is free from the valve floor in some *Megathyris*, in others confluent with it. The loop appears to run over the ventral surface of the lateral septa while these are still tiny, its anterior edge projecting as described for the medium septum, yet may be fused with them. In the region between the lateral septa and the crura the descending branches may either be free from the valve floor or confluent with it, in the latter instance the anterior ends of the posterior part of the loop and the posterior ends of the anterior part seem to disappear into the valve floor. The descending branches have a somewhat chalky appearance compared with that of the valve floor, and are exceedingly thin and delicate.

I am indebted to M. Paul Bougis for sending me megathyrids from Banyuls-sur-Mer, and to Dr A. J. Southward and the Captain and crew of R.V. 'Sarsia' for *Megathyris*. The work was done whilst occupying a London University Table and part of it with assistance from the Browne Research Fund of the Royal Society, 1956–57.

SUMMARY

The structure of the adult lophophores of *Argyrotheca* and *Megathyris* is described. In megathyrids the filaments are in a single series and all of the same type. The ciliary feeding mechanism differs from that previously described by the writer in brachiopods in that in addition to reversal of the frontal cilia, reversal of the inhalant and exhalant currents occurs.

The behaviour of *Argyrotheca cordata* during the escape of larvae from the brood pouches is briefly described.

Certain of the growth stages of the shell and of the lophophore and loop of *Megathyris* are described and figured. *Megathyris* passes through a schizolophous stage resembling the adult lophophore of *Argyrotheca*.

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ON THE BIOLOGY OF *CRANGON ALLMANI* KINAHAN IN NORTHUMBERLAND WATERS

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(Text-figs. 1–15)

Since November 1954, the natant epifauna in depths greater than 20 fm. off the Northumberland coast has been sampled at a number of stations with the object of obtaining information on its constitution and fluctuations. The survey has been limited to those species caught with a net of $\frac{3}{4}$ in. mesh. Seasonal and yearly fluctuations in this fauna must have a considerable effect on the inshore fisheries, for these animals form an important part of the food of marketable fish, yet, this fauna has never been subject to a detailed analysis over a number of years.

Samples have been taken as regularly as weather and other laboratory commitments have allowed. In practice this has been of the order of one sample each month, but at times sampling has been more frequent than this (Table 8). Although sampling is being continued, the material collected so far gives much information on the epifauna as a whole and the biology of the constituent natant Crustacea and Mollusca.

It was soon clear that the best method for dealing with the samples was to analyse the biology of each of the commoner species in turn before reviewing the data as a whole. *Pandalus borealis* was the first species to be so considered (Allen, 1959). The second choice is *Crangon allmani* Kinahan*. *C. allmani* has been chosen for the following reasons: (1) it is one of the more common offshore species of natant decapod in Northumberland waters; (2) in contrast to *Pandalus borealis* (Allen, 1959) it occurs throughout the area below 10 fm.; (3) it forms an important item of food for many marketable fish including the Whiting (Todd, 1907; Jones, 1954); Haddock (Ritchie, 1937; Jones, 1954); Thornback Ray and Long Rough Dab (Todd, 1907) and others; and (4) virtually nothing is known of its biology.

While earlier authors doubt whether *Crangon allmani* is more than a subspecies of *C. vulgaris* (Doflein, 1900; Ortmann, 1891) observations by Wollebaek (1908) on the adult and by Sars (1890) and Lebour (1931) on the larvae show that it is a distinct species. This study gives further emphasis to the differences between the two species and presents an opportunity to correct the original descriptions of Kinahan (1857, 1861) and to figure the external anatomy more fully than hitherto.

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* Kinahan (1857) named this shrimp *Crangon allmanni*. This is clearly a *lapsus calami* and the specific name should be spelt *allmani*.

I wish to thank Mr R. Harrison and the crew of the research vessel 'Alexander Meek' for collecting in all weathers. I am also grateful to Dr H. O. Bull for the use of his hydrographic data and for the helpful discussions during the course of the work, and to Dr R. B. Pike for information on the Clyde populations.

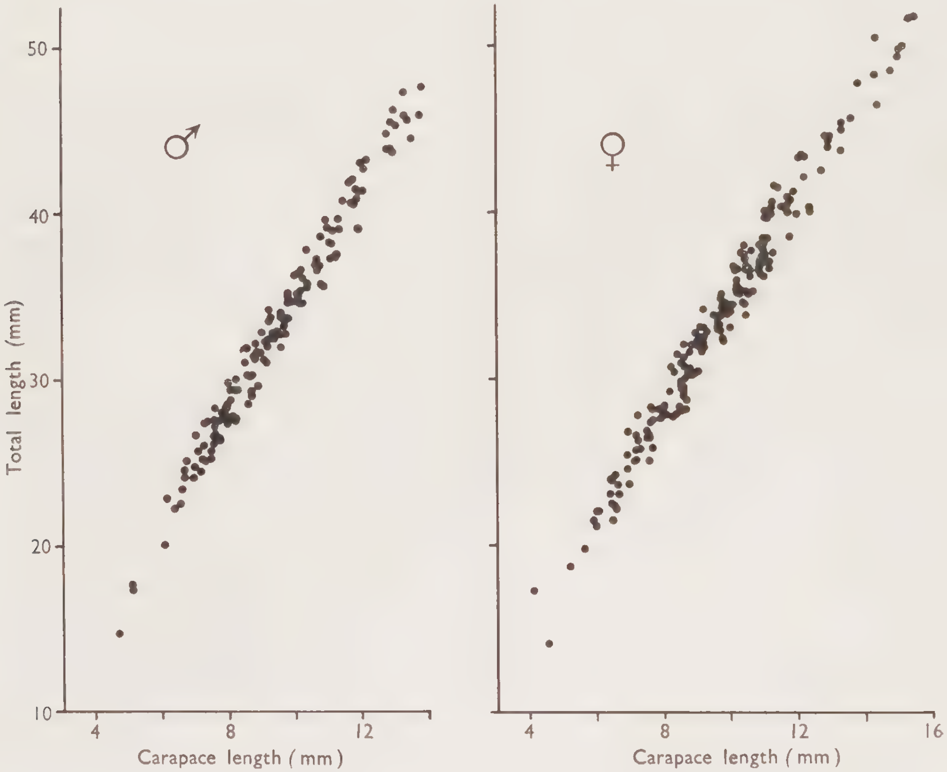

Fig. 1. Relationship between carapace length and total length in male and female *Crangon allmani*.

MATERIAL AND METHODS

Throughout this work a 9 ft. trawl has been used. Until March 1956 a beam Trawl was used, but since that date an Agassiz trawl has been preferred. Each haul was of 20 min duration. The catch was sorted and, apart from a few specimens retained for observations in the aquarium, narcotized in fresh water, fixed in 4% neutral formalin for approximately 12 h and then transferred to 90% alcohol.

Later, length measurements were taken, sex determined and when eggs were present these were classified under one of the following four groups: *a*, early blastoderm; *b*, late blastoderm and early segmentation of the body; *c*, eye visible but abdomen not free from the head; *d*, well-developed abdomen and little yolk present. Specimens with egg remains and the larvae recently released, those in breeding dress and recently moulted shrimps were all recorded. Approximately 5% (over 400) of the total number of *C. allmani* caught were retained for further examination. These animals were representative of the size range, sex and maturity within each sample. Each animal of the subsample was remeasured, pleopods examined and usually drawn to scale, gut contents examined, and maximum ova length recorded. Eggs were classified, counted and measured. Drawings were made of the appendages and body of males and females of varying sizes. The ratio of carapace length (tip of the lateral carapace spine to the posterior limit of carapace, see Fig. 12) to total length (tip of the rostrum to the tip of the uropod setae) was calculated (average 3·49, limits 3·23–3·71). This relationship was found to be linear, there being no significant difference between males and females (Fig. 1). It was found that the lateral spine of the carapace (Fig. 12) was a far more accessible anterior point of reference for measuring carapace length than the more usual posterior limit of the eye socket; only rarely was the spine found broken. Measurements were carried out with a vernier caliper and taken to the nearest 0·1 mm.

DISTRIBUTION

C. allmani is restricted to the eastern boreal region of the Atlantic. According to the literature, it extends from the White Sea to the northern part of the Bay of Biscay. It has been recorded for Iceland, it is present throughout the North Sea and the Kattegat and is found off all the coasts of Great Britain. It is apparently least plentiful off the south coasts of England and Ireland. In Danish waters and occasionally elsewhere it occurs in as little as 5 fm. of water, but its normal range extends from 10 to 100 fm. Off the Northumberland coast *C. allmani* has been taken at all depths below 9 fm. on every type of bottom with the exception of rock. The density of the population at any particular point may vary enormously. The 10 fm. contour line (see Fig. 2) is the approximate offshore limit of *C. vulgaris* and, at certain times mixed populations occur at this depth. There has never been the slightest difficulty in separating the two species; colour, body shape and the bicarinate dorsal side of the sixth abdominal segment of *C. allmani* being infallible diagnostic characters.

During this study three main stations, A and B (inshore) and C (offshore), were sampled (Fig. 2). Originally sampling started inshore (St. A) two miles due east of Blyth Harbour in 25 fm. Soon after, the offshore station (St. C)

13 miles due east of this harbour in 50 fm. was sampled. By the autumn of 1955 hopper refuse had fouled the 2 miles station, even though this was a mile inshore of the dumping grounds. This colliery refuse virtually wiped out the fauna and the ground became impossible to trawl over, so that a second inshore station (St. B) was sampled 1·9 miles, 050° from Newbiggin Church in 22 fm. Additional samples have been taken throughout the area indicated in Fig. 2, but unless otherwise stated the data presented are from samples collected at the three stations.

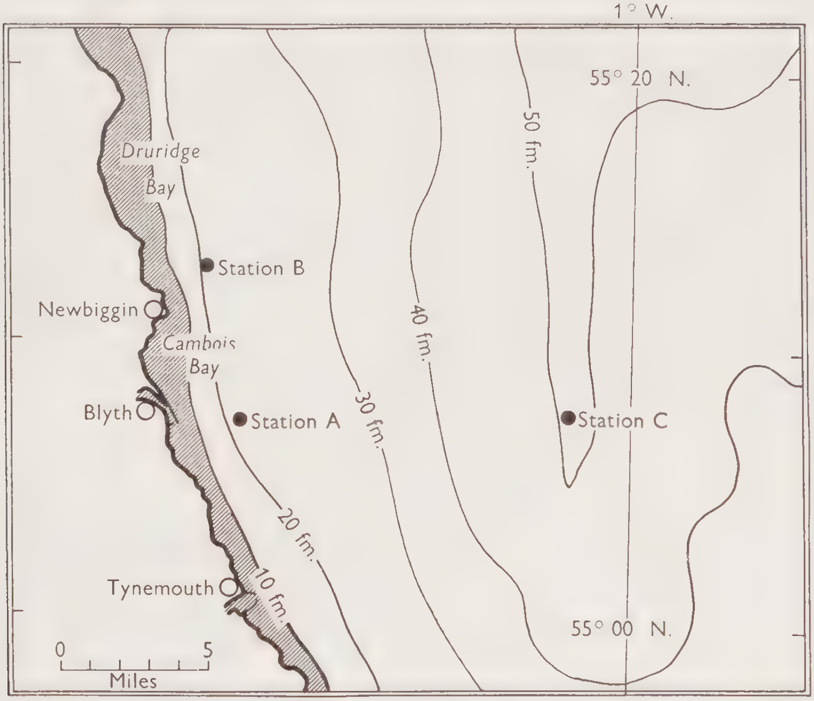

Fig. 2. The area investigated with the position of the Stations A, B, and C indicated. *Crangon vulgaris* is restricted to the hatched area and *C. allmani* to the non-hatched area.

Samples taken inshore during the first year showed a marked drop in the numbers of *C. allmani* caught during April and May (Fig. 3). This drop in numbers persisted throughout the summer and autumn months (May-October) and has proved to be a constant yearly occurrence at the inshore stations and elsewhere between 10 and 30 fm. Offshore *C. allmani* did not disappear during the summer months but it is clear that shrimps in 40–50 fm. are not evenly distributed and hauls without or with very few shrimps were taken throughout the year (Table 8). That the trawl was fishing on these occasions is indicated by the presence of normal numbers of other members of this

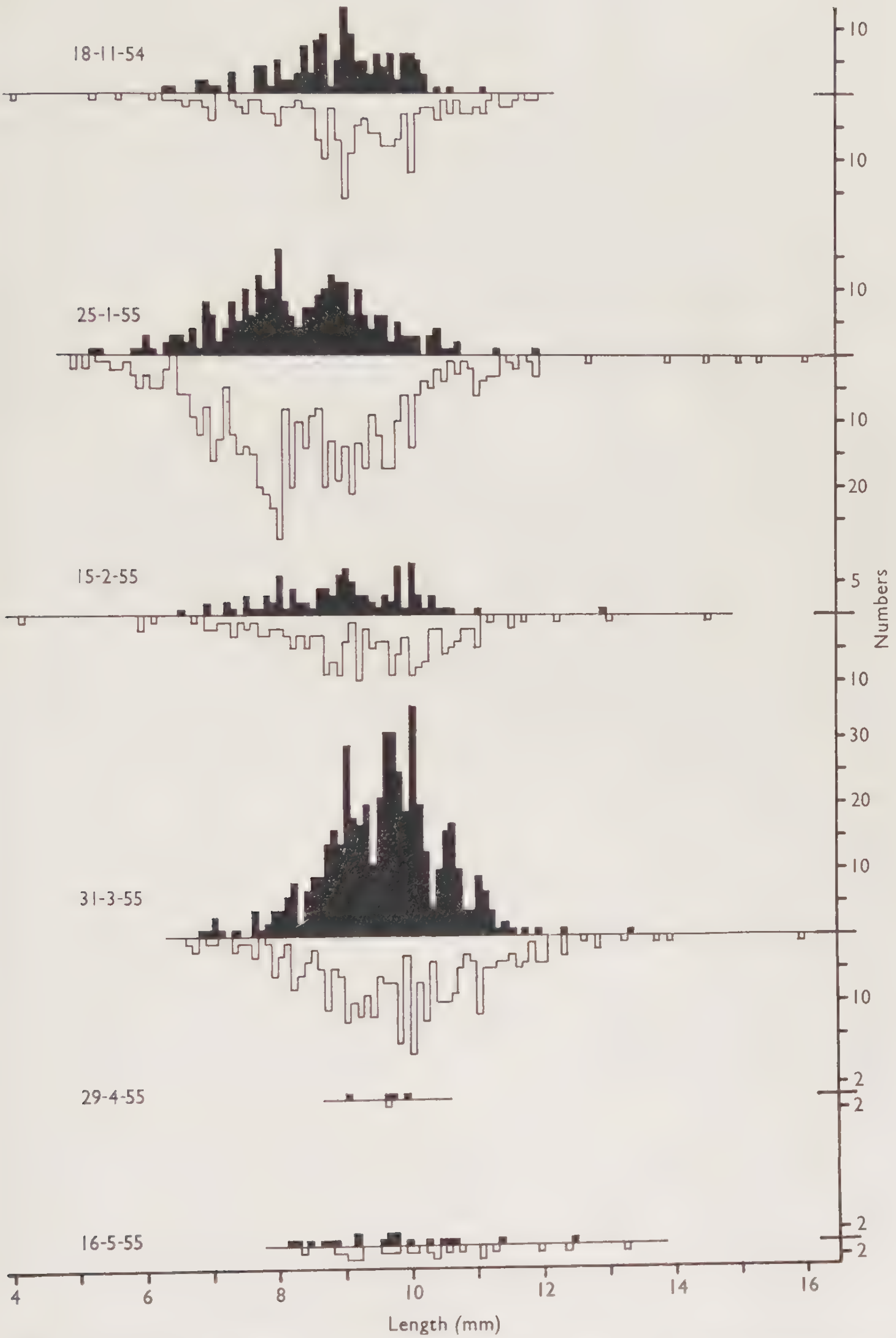

Fig. 3. Population histograms, in carapace-length groups, of the samples taken from Station A between November 1954 and May 1955 Males (black) above and females (outlined) below the line.

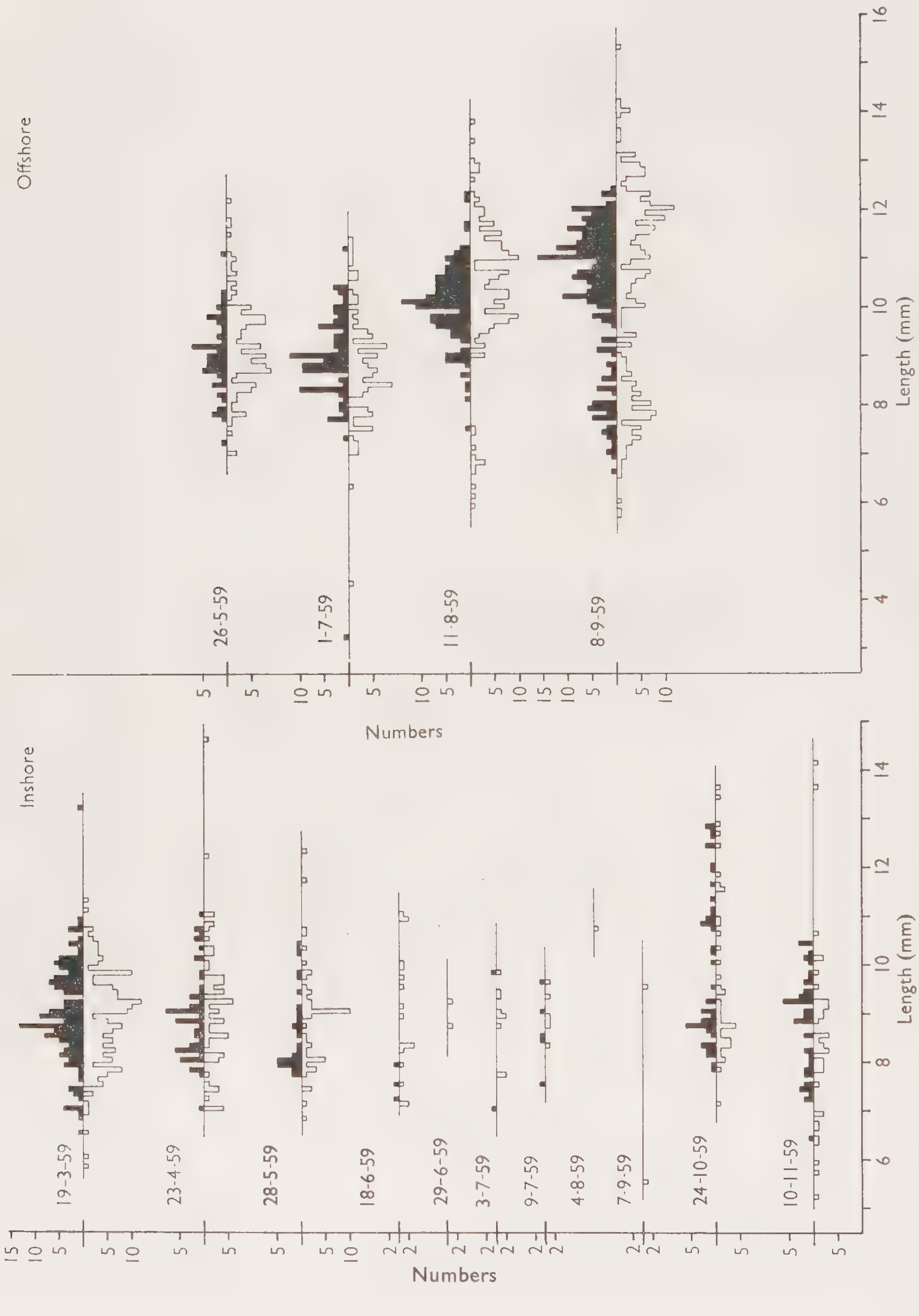

Fig. 4. Comparison of inshore (St. B) and offshore (St. C) population histograms during 1959. Males (black) above and females (outlined) below the line. The length given is that of the carapace.

epifauna. This difference between inshore and offshore populations was closely observed in 1959 (Fig. 4) when the trawling effort was increased in order to make sure that the inshore population had largely disappeared. Sampling outside the main stations indicates that this seasonal change can be observed in depths up to 35 fm. In this connexion it is of interest that examination of stomach contents of Whiting caught in the same area during 1953 to 1955 from depths of 20 to 30 fm. shows that while the fish are feeding predominantly on *C. allmani* during the months October to April few shrimps are present in the stomach contents from May to September (Goonewardene, unpublished*). Although there is lack of direct evidence, there can be little doubt that the disappearance is the result of a migration. This will be assumed in the pages preceding the discussion of this point.

BREEDING

C. allmani is a dioecious species. Offshore, the average ratio of males to females was 0·98–1·00 but with a wide range of 0·49–1·12 to 1·00. Inshore, there are on the average far fewer males than females, the ratio being 0·62–1·00, with the range being even wider than offshore 0·15–1·38 to 1·00. This point will be further discussed when evidence for migration is presented (p. 503).

TABLE 1. AVERAGE MONTHLY PERCENTAGES OF THOSE FEMALE *CRANGON ALLMANI* IN BREEDING DRESS (*bd*), THOSE BEARING EGGS AT STAGES *a*–*d* AND THOSE WITH EGG REMAINS FOLLOWING THE RELEASE OF THE LARVAE (*lr*)

	bd	*a*	*b*	*c*	*d*	*lr*
Nov.	—	—	—	—	—	—
Dec.	6·0	1·5	—	—	—	—
Jan.	0·8	13·8	6·0	0·9	—	—
Feb.	0·5	4·6	4·9	0·7	1·8	—
Mar.	1·0	12·4	11·9	6·1	2·8	2·7
Apr.	—	26·6	34·7	4·7	—	7·6
May	1·0	26·7	13·9	9·3	2·1	11·8
June	—	14·3	21·4	7·1	14·3	28·6
July	—	31·0	1·7	—	—	0·4
Aug.	—	—	—	—	—	0·9
Sept.	—	—	—	—	—	—

The percentages are calculated on total number of females per haul, i.e. no account is taken of immature females (see below).

Females bearing eggs first appear in small numbers (1·5% of all females†) by the end of the first week in December. All the eggs are at stage *a*. By

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* University of Durham, Ph.D. Thesis, 1956. 'The biology of the Whiting (*Gadus merlangus* Linn.).

† The percentages, unless otherwise stated, including those of Table 1 are based on the total number of females in the catch, i.e. including immature females less than 7·5 mm carapace length. The percentage of immature females is small (Table 2) and does not affect the results presented.

TABLE 2. THE AVERAGE MONTHLY PERCENTAGE OF IMMATURE FEMALE *CRANGON ALLMANI* (LESS THAN 7·5 MM CARAPACE LENGTH) AND AVERAGE MONTHLY PERCENTAGE OF FEMALES GREATER THAN 7·5 MM CARAPACE LENGTH THAT ARE OVIGEROUS: INCLUDING THOSE IN BREEDING DRESS AND WITH EGG REMAINS AS WELL AS THOSE BEARING EGGS.

	(%) Immature females	(%) Ovigerous females		(%) Immature females	(%) Ovigerous females
Dec.	1·5	7·6	June	10·0*	55·0*
Jan.	12·1	24·2	July	2·9	31·4
Feb.	6·3	11·1	Aug.	7·2	1·9
Mar.	4·2	31·9	Sept.	8·6	—
Apr.	6·1	55·9	Oct.	7·4	—
May	2·9	49·1	Nov.	12·3	—

* Percentage calculated on less than thirty specimens.

the end of January 13·8 % of all females bear eggs at stage *a*, 6·0 % at stage *b* and a few, less than 1 %, are eyed and at stage *c*. Advanced larvae at stage *d* are present (1·8 %) in the mid-February samples but females that have released their larvae are not seen until the first week in March (Table 1). It appears that eggs laid at the beginning of the breeding season are carried for about 10–12 weeks. During February there is a decrease in the number of females with recently laid eggs. The percentage of females bearing stage *a* eggs increases during March and reaches a peak of more than 26 % during April and May. There is a decrease in June and another peak is recorded in the offshore population in July. No females bearing stage *a* eggs have been recorded after mid-July. In fact no egg-bearing females have been taken after July although a small number of females with egg remains were taken in August (Table 1). Thus it would appear that eggs laid early in July hatch 5 or 6 weeks later, i.e. their development is twice as fast as those laid at the beginning of the breeding season. This increase in the rate of egg development as the breeding season advances is supported by the fact that while the greatest percentage of eggs at stage *a* is reached in April and May, it is the June samples that show the greatest percentage of females bearing stage *d* eggs and newly hatched larvae (14·3 and 28·6 %, respectively). This indicates a development time of about 7 weeks. Such a decrease in development time has been recorded by Havinga (1930) in the case of *C. vulgaris*. He calculated that the winter (October–November) brood of *C. vulgaris* at a temperature of about 9° C take about 9 weeks for development while the summer eggs (May–June) at a temperature of about 18° C develop in half that time. This relationship to temperature is by no means so clear in Northumberland waters. From December to March there is an average drop in the temperature of the offshore water close to the bottom of 9·0–5·5° C and inshore 9·0–5·0° C (Fig. 5). From March to July there is a corresponding increase in temperature from 5–10° C inshore and from 5·5–7·5° C offshore. The range in temperature is much the same for the two halves of the breeding season, even though the population that is inshore at the beginning of the breeding season has moved offshore during the second half of the season. That the temperature is falling in the first period and rising in the last may be

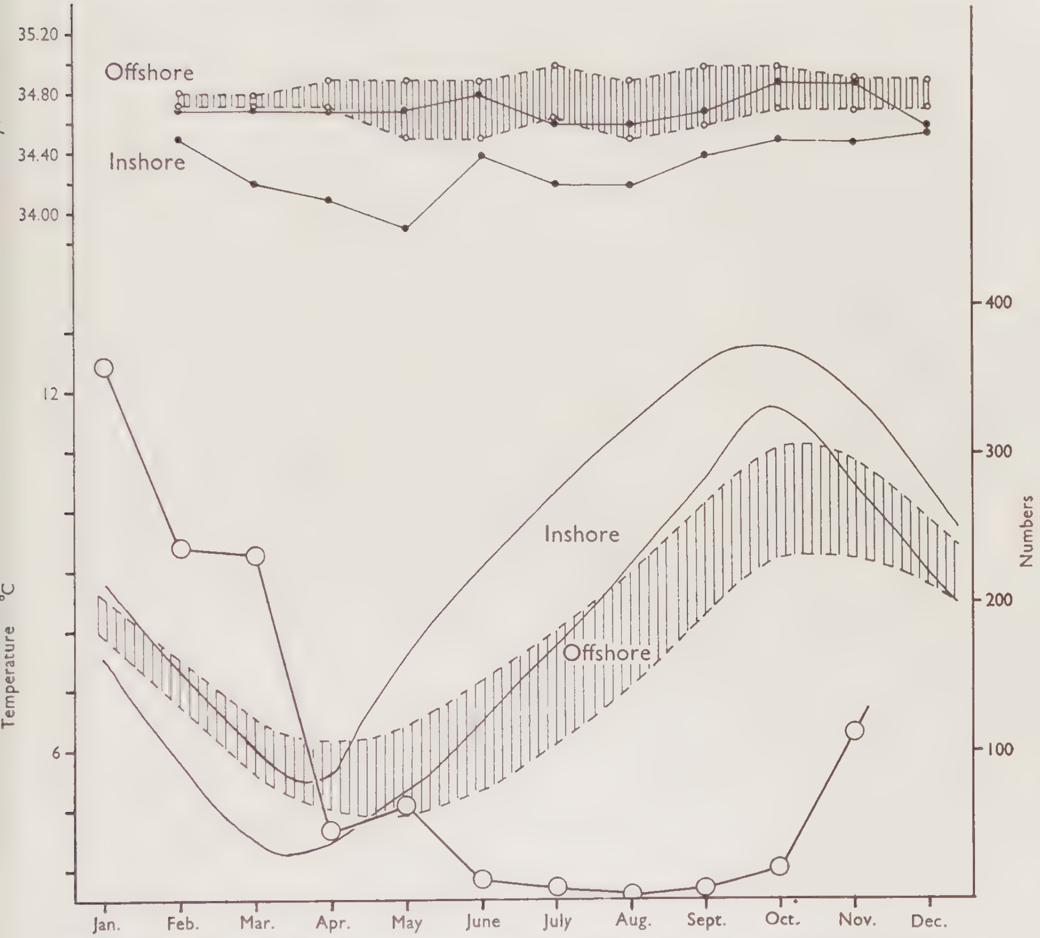

Fig. 5. The limits of salinity and temperature records from deep water inshore (25–30 fm) and offshore (45–50 fm.) during the years 1953–58. The inshore average monthly catch per 20 min haul of *C. allmani* is superimposed on the hydrographic data.

of significance. Broekema (1941) finds that salinity is related to egg development time in *C. vulgaris*, but in the case of *C. allmani* salinity changes during the breeding season cannot compare with those experienced by *C. vulgaris* in shallow and estuarine waters. Broekema finds that development may be twice as long in salinity of 16‰ as compared with 35‰ in the case of

C. vulgaris and that with increasing temperature the salinity optimum shifts towards less saline water. The maximum range in salinity of the bottom water at the inshore stations is 34–35‰, with minimum salinities in May and June and maximum in November and December. Offshore the range is less—34·5–35·0‰ and seasonal changes are not clearly seen (Fig. 5). During July to October, the period of maximum water temperatures, *C. allmani* is offshore in water of relatively high salinity, but it seems very unlikely that such a small salinity range can have any effect on egg development time. Small salinity changes might conceivably have an effect on migration. It may be that there is a difference in the eggs of the two broods that would account for the difference in development time. Ova have taken 6 months to develop in the case of the first brood and only 3 months for the second brood. Although egg diameter remains constant throughout the breeding season there may be a difference in yolk content.

Jørgensen (1923) found *C. allmani* larvae in Northumberland waters. Her sampling commenced in May so unfortunately there are no records for January to April. Larvae were most numerous in the Blyth and Newbiggin area during May and there was a second hatching period from the end of July until September. It is possible that the latter period corresponds to the final burst of egg laying in early July. Bossanyi (1957) also records larvae of *C. allmani* from April to July 1½ miles offshore in Cambois Bay (Fig. 2) in depths from 13 to 15 fm. Information on the breeding elsewhere in British waters is similar to that above. Lebour (1931) states that breeding starts in the Plymouth area in January, early larval stages being present in the plankton from January to June and late larval stages through spring and summer. This would perhaps indicate that, in the Channel, development is more rapid in the early part of the breeding season than in Northumberland waters. Dr R. B. Pike, in a personal communication, confirms that the breeding season of the Clyde population is comparable with that of Northumberland, while Kemp (1910) reports that ovigerous females are to be found off coasts of Ireland from January to May. Elsewhere, in Scandinavian waters breeding appears to be somewhat later than in British waters. Thorsen (1946) records larvae from April to July in the Kattegat, while Björck (1913) from the same water found berried females with early eggs in July and with late eggs from late July to early October and larvae over the same period. In West Norway (Wollebaek, 1908) berried females are found in March and throughout the summer, the larvae hatching during the summer months.

Analysis of the length measurements of the egg bearing females shows a decrease in average length over the breeding season although the overall size range does not differ over the season (Table 3). Only three specimens with a carapace length of less than 7·5 mm (one at 7·1 mm and two at 7·4 mm) were found carrying eggs. The majority of shrimps between 7·0 and 7·5 mm carapace length were obviously immature and this was confirmed when ovum length was plotted against carapace length in non-ovigerous females (Fig. 6). Examination of the testes shows that the male matures at about the same size as the females, so that for purposes of calculation shrimps below 7·5 mm carapace length are classified as immature.

TABLE 3. THE CARAPACE LENGTH IN MM OF FEMALE *CRANGON ALLMANI* BEARING EGGS FOR EACH MONTH OF THE BREEDING SEASON

	Average	Range		Average	Range
Dec.	10·5	(10·5)	Apr.	9·8	(6·9–12·1)
Jan.	11·3	(8·0–16·0)	May	9·3	(7·7–13·2)
Feb.	10·1	(7·4–14·8)	June	9·6*	(7·1–11·1)
Mar.	10·3	(7·9–16·9)	July	9·6	(7·9–12·4)

* Calculated on less than thirty specimens.

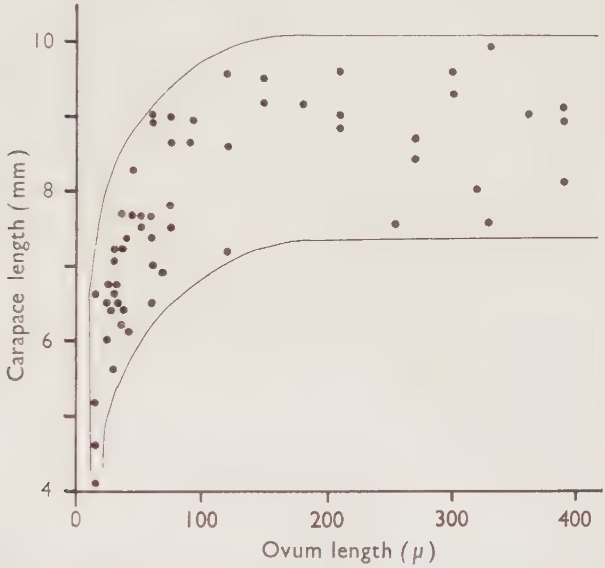

Fig. 6. Carapace length plotted against ovum length in females that have yet to lay eggs.

Little growth of the ova occurs before *C. allmani* reaches 5·5 mm carapace length. There is a marked increase in the rate of growth of the ova after the shrimp has grown to 6·5 mm and exceptionally eggs are laid soon after it reaches 7·0 mm carapace length (Fig. 6). The majority of the females do not develop so fast and first lay their eggs when the carapace measures between 8·5 and 9·5 mm. As the breeding season extends over 7 months and there appear to be two, or possibly three, peaks of egg laying, it was necessary to find whether the shrimps lay more than one brood during the season. Ovum length was plotted against stages in egg development (Fig. 7). Not all the ova are released at the time of the first egg laying. There remains a core of small ova each approximately 50 μ long that increases rapidly in size during the period of egg carriage so that when the larvae are released a second brood is almost ready to be laid, the ova being approximately 370 μ long. In *Pandalus borealis* (Allen, 1959) the growth rate of the ovum in the latter half of its development in the ovary was shown to be a straight line. This also appears to be the case in *C. allmani* and extrapolation of the graph indicates that the interval between release of the larvae and the re-assumption of breeding dress and the second egg laying is of the order of 2 or 3 weeks. The growth rate of the ova of egg-bearing females in the June and July samples is not rapid. The reduction in the growth rate is maintained during the late summer and autumn and the ova take 6 or 7 months to reach maturity as compared with 3 months for the second brood of the season (Fig. 8).

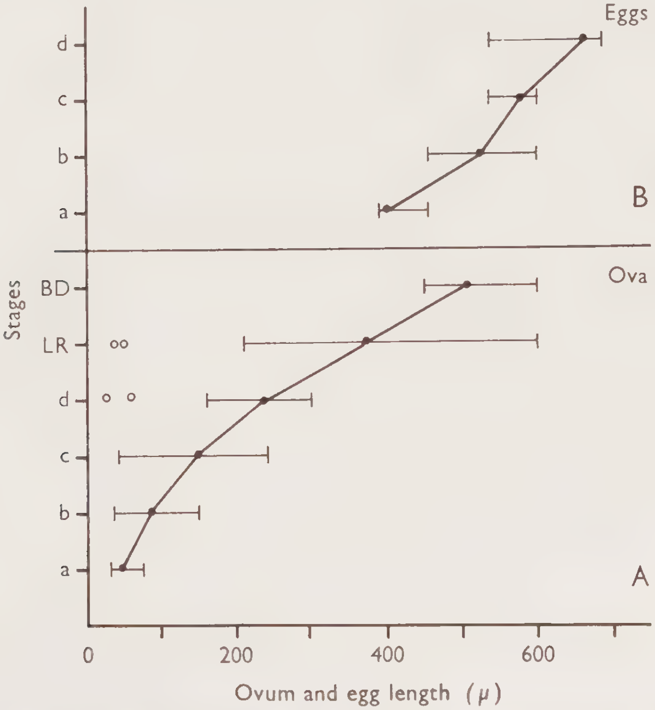

Fig. 7. To show, A, growth of the ovum during the development of the egg and, B, the increase in length of the egg during its development. ○, indicates the length of the ova in females with eggs ready to hatch during June and July. BD, breeding dress; LR, egg remains following the release of the larvae; see p. 483 for explanation of stages *a*, *b*, *c* and *d*.

The ovary of the immature shrimp extends from the posterior end of the stomach to the dorsal posterior limit of the carapace, while that of the female with mature ova extends from the anterior limit of the carapace to the centre of the third abdominal segment. Egg laying usually occurs shortly after the assumption of breeding dress. Most of the females caught in breeding dress were soft and so were many with newly laid eggs. The newly laid eggs are a transluscent gold colour and are remarkably constant in size irrespective of differences in the time taken for the ova to mature. They are spherical when first laid with a diameter of 390 μ. The eggs soon elongate and continue to do so throughout their development. Immediately before hatching the egg case is approximately 650 μ long (Fig. 7). It will be noticed (Figs. 7, 8) that the length of the mature ovum is greater than the diameter of the newly laid egg. This is due to the compression of the ovum within the ovary producing an elongate, angular shape.

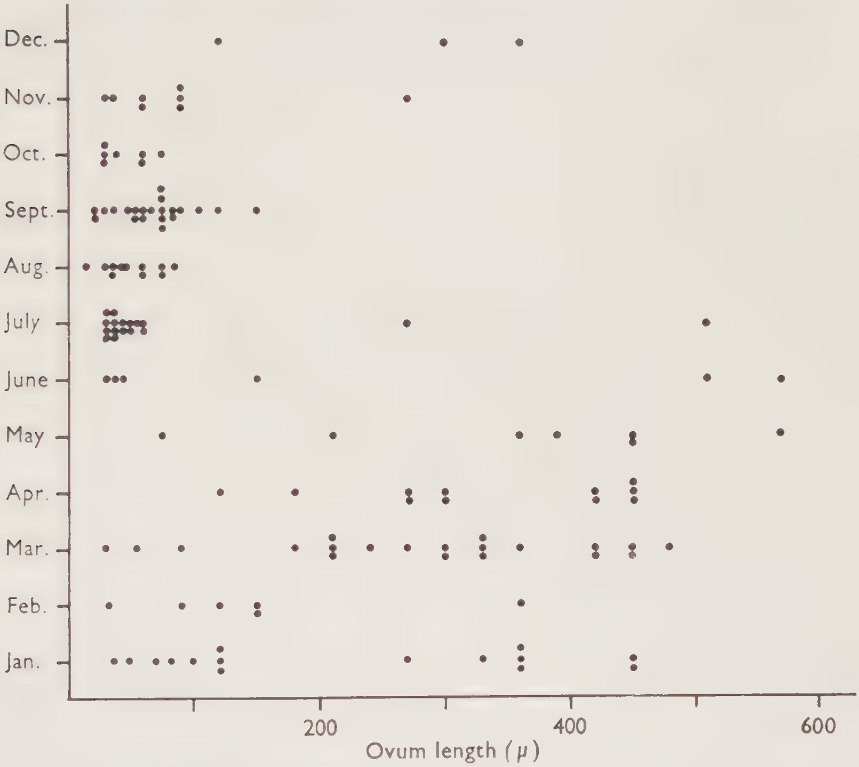

Fig. 8. Maximum ovum lengths in ovigerous females, or non-ovigerous females that have had at least one brood of eggs, plotted against month of capture.

Høglund (1943) shows that owing to the weakly developed epimera, short basipodites and endopodites, with the latter lacking stylamblys, the eggs of *Crangon* are more exposed and unprotected than those of any other caridean. This makes heavy demands on the fixing system and in *Crangon* the ovigerous setae and the cement are particularly strong. Nevertheless, the eggs of *C. allmani* are easily detached and the possibility of loss increases with age as the developing eggs enlarge with the resulting increase in volume of the egg mass. Many shrimps with advanced eggs appeared to have considerably reduced numbers and for this reason egg counts were taken only in the case of females with stage *a* eggs. The average egg count for females with a carapace length of 7·5 mm is 400 and this increases to approximately 2500 on a shrimp 13·0 mm long. The largest female taken (17·0 mm) carried 7060 (Fig. 9). Although they carry relatively large numbers of eggs, females of carapace length greater than 13·0 mm represent such a small percentage (2%) of the breeding stock that they play only a small part in maintaining the population. The eggs are carried on the first four pleopods and on pereiopods 4 and 5 as they are in *C. vulgaris* (Yonge, 1955) and in both species, the forward extension of the egg mass under the thorax is probably a modification related to the bottom feeding.

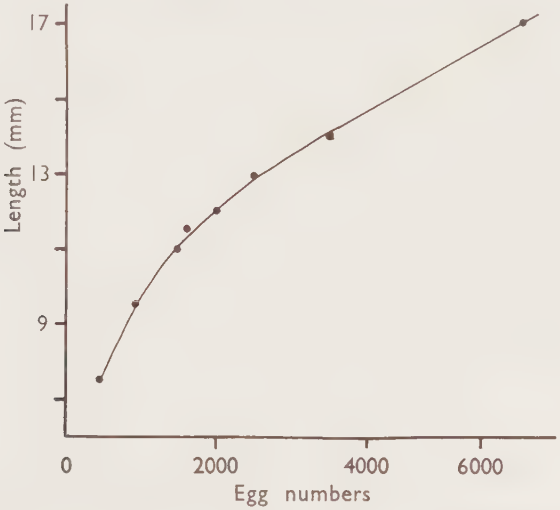

Fig. 9. The average number of eggs carried by *Crangon allmani* at various carapace lengths.

GROWTH

A prolonged breeding season with three breeding maxima makes it very difficult to decipher the monthly population histograms for the purpose of abstracting information on rate of growth (Figs. 3, 4). Furthermore, owing to the size of net used, few *C. allmani* smaller than 6·0 mm carapace length were caught. Dredge samples secured a few young *C. allmani* mainly during the months July to September. These had an average carapace length of 3·5 mm. As the carapace length of the newly metamorphosed *C. allmani* must be of the order of 2·0 mm (the last larval stage is 6·5 mm long—Lebour, 1931), there can be little doubt that these are recently hatched 0-group. This group appeared in the trawl hauls inshore in November when a few females between 4·0 and 6·0 mm carapace length were caught. By January the average carapace length of the 0-group is 6·0 mm (Fig. 10). Although the youngest *C. allmani* are too small to be retained in the net in any numbers, a few specimens below 6·5 mm carapace length are caught throughout the year and it is probable that recruitment is continuous from April to October with the main peak from July to September. The only samples showing two clearly defined population peaks are those offshore in September (Fig. 4). One peak has an average carapace length of 8·0 mm (1-group) and the other 11·5 mm (2-group). Peaks corresponding to the 8 mm 1-group are not seen in histograms of offshore samples in the following months and it is probable that this group migrates inshore during October and forms the greater part of the inshore population in the November samples (Fig. 3). This population has an average carapace length of 8·7 mm. November is the first month following the seasonal disappearance when *C. allmani* is taken in large numbers inshore. Some of the larger 2-group *C. allmani* also move inshore, mainly during December and January. Owing to the small numbers involved, differences between the rates of growth of males and females, are not apparent in shrimps less than 7·5 mm. The females of the inshore samples (mainly 1-group) from January to May show little increase in size, the average carapace length being 9·3 mm. This

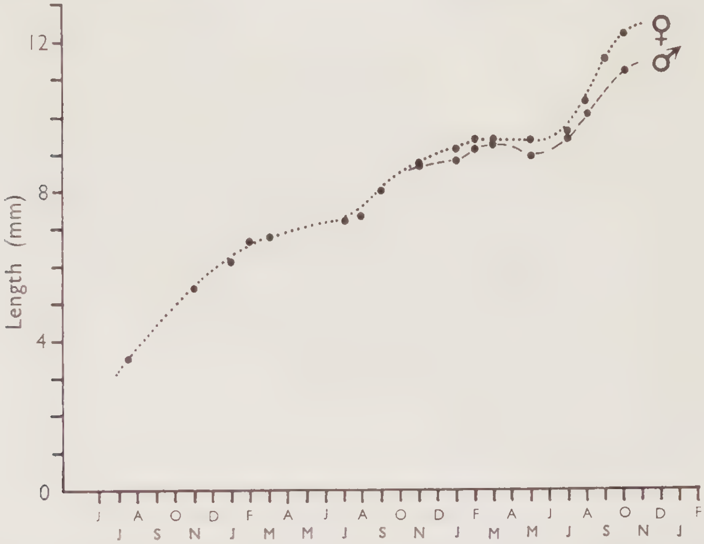

Fig. 10. The probable growth-rate curve of male and female *Crangon allmani* during their normal life span: mean carapace length plotted over a period of 2½ years.

lack of growth is no doubt due to the cessation of moults while egg bearing. The effect of the growth of shrimps maturing for the first time and also the continued entry of 0-group into the catches is offset by the interbrood growth. There is a gradual but slow increase in the average size of the males during January to March (8·8–9·3 mm) followed by a drop in April and May (8·9 mm). This drop is probably due to the effect of the offshore migration. During April and May the inshore population almost completely disappears, and it is probably significant that May is the only month in which the average length of the inshore and offshore populations is the same (Fig. 11). During the rest of the year the average length of the offshore population is greater than the inshore. In the period May to October a few *C. allmani* remain inshore. These are mostly small females about 8·5–9·0 mm carapace length (Table 7). During the same period offshore there is a steady increase in the average length of the population (Figs. 4 & 11), and by the end of the period the original 1-group and 0-group have become the new 2-group and 1-group, respectively. The new 2-group reaches a maximum average size of 12·5 mm in November, after which there is a drop probably due to the death of the largest shrimps following early spring breeding (see below).

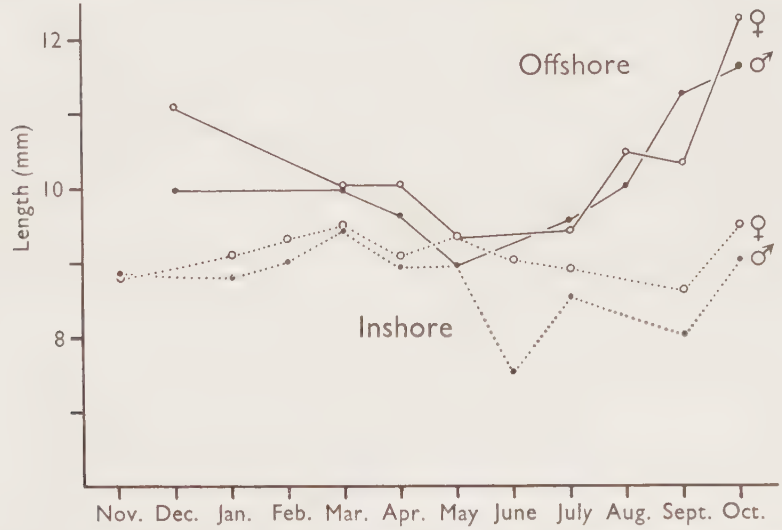

Fig. 11. Comparison of the average carapace length of the *Crangon allmani* caught inshore and offshore throughout the year.

Throughout life the male *C. allmani* is slightly smaller than the female. The females of the new brood are the first to appear in the catches, but the difference in the average carapace lengths is never greater than 1·0 mm in the oldest shrimps. Comparison of the mean lengths of the males and females of each haul does not necessarily give a true figure for this difference in size. The two sexes appear to migrate at different times with the result that in some samples (e.g. offshore, September) the average length of the male is greater than the female (Fig. 11). Although most of the *C. allmani* die in their third year a few live at least one more year. The largest female caught was 17·0 mm carapace length and the largest male 14·0 mm. The male probably dies before the female, soon after copulation. Further examination of the data suggests that many 2-group shrimps which form a large part of the breeding stock during December to March die and do not breed a second time. It is interesting to note that Wollebaek (1908) reports that the average size of *C. allmani* in Norwegian waters is larger than that of *C. vulgaris* (100 mm as to 60–70 mm). The reverse is true in British waters.

MOULTS

The records of recently moulted shrimps show no significant difference between males and females from inshore or from offshore grounds. On the average, 4 % of all *C. allmani* have recently moulted. There is some difference between the samples taken between January and June (3·1 %) and July to December (6·6 %). Such a difference might be expected as the former period covers the breeding season when egg bearing restricts moulting while the latter is the period of maximum growth when the new year group is entering the stock. Most of the specimens in breeding dress are soft as are many of the females bearing newly laid eggs. The data give no indication how frequently *C. allmani* moults, except that 9·0 % of those less than 8·0 mm carapace length, 4·8 % of those between 8·1 and 10·0 mm and 3·4 % of those greater than 10·1 mm had recently moulted.

In the interval between successive broods there is a moult to dispose of the old breeding dress and egg remains followed by re-assumption of breeding dress within a maximum of 3 weeks. It is known that the moult frequency of other Caridea of similar size is about 20–35 days (Nouvel & Nouvel, 1937; Høglund, 1943) so that it seems unlikely that there are intermediate moults between the losing of the old and the gaining of the new breeding dress.

FOOD

The analysis of the stomach contents of more than 350 *C. allmani* is shown in Tables 4 & 5. Approximately 54 % had food in the stomach. It will be seen from Table 4 that there is little difference in the percentages of shrimps with and without food in respect of sex and of maturity of the gonads. Females, with mature gonads taking all the available space in the thorax, had food present. Only in newly moulted shrimps was food invariably absent. Identification of the food proved far from easy as the mandibles (Fig. 12), which are both large and efficient, break the food into small fragments.

TABLE 4. THE PERCENTAGE OF *CRANGON ALLMANI* WITH FOOD PRESENT IN THE STOMACH WITH RESPECT TO SEX AND MATURITY

	Number examined	Percentage with food	Percentage without food
Male	150	52·7	47·3
Female	200	55·0	45·0
Immature testis	82	57·7	43·3
Mature testis	68	50·0	50·0
Females without eggs	147		
With ova length $< 150\mu$	101	52·5	47·5
With ova length $> 150\mu$	46	56·5	53·5
Females with eggs	52	55·8	44·2

The sample is representative of the size range.

C. allmani feeds predominantly on living Crustacea and Annelida. Mollusca, Foraminifera and Ophiuroidea are present in smaller quantities, while Whiting scales were present in a few stomachs. Sand and mud particles are always present with the food. In the laboratory the shrimp behaves in much the same way as *C. vulgaris* (Lloyd & Yonge, 1947), burrowing and searching in the top few millimetres of the substratum. Occasional specimens were taken with a small *Nephthys* held by the mouth parts. The chelae, maxillae and maxillipeds appear to be used for grasping and guiding the food into the mouth, the mandibles alone are used in mastication, although Havinga (1929) refers to 'chewing teeth' on the first maxilla in *C. vulgaris*. Identifiable annelidan remains consist of *Nephthys* (*ca.* 90 %) and *Glycera* (*ca.* 10 %). The crustacean remains are more varied and consist of small Cumacea, Amphipoda, Copepoda and young *C. allmani*. Of the identifiable Mollusca the most common were *Dosinia lupinus*, *Venus striatula* and *Cylichna cylindracea*.

TABLE 5. PERCENTAGES OF DIFFERENT TYPES OF FOOD ORGANISMS PRESENT IN STOMACHS OF *CRANGON ALLMANI* FROM INSHORE AND OFFSHORE STATIONS

	Inshore		Offshore	
	♂	♀	♂	♀
Crustacea	65·6	68·1	55·6	63·9
Annelida	43·1	43·1	59·3	61·1
Mollusca	12·1	16·7	7·4	5·6
Foraminifera	3·9	4·2	11·1	—
Ophiurida	1·7	1·4	—	—
Whiting scales	6·9	4·2	—	—
Without food	43·6	43·7	44·9	49·4
With food	56·4	56·3	55·1	50·6

Comparison of the stomach contents of the inshore and offshore populations shows a few differences. About 65 % of the shrimps with food in the stomach have crustacean remains, with little difference between the two populations. Significantly more worms are eaten offshore (60 %) than inshore

(43 %), while more molluscs are eaten inshore than offshore (Table 5). Other food organisms are in too small quantity to make any comparison except that it should be noted that Whiting scales were only present in the stomachs of *C. allmani* from the inshore stations. There is no significant difference between the diet of the male and the female.

Analysis of food with respect to size and month of capture shows little variation in either case except that the smaller size groups have a high proportion of copepods in their crustacean food.

EXTERNAL MORPHOLOGY

The woodcuts of *C. allmani* illustrating the original descriptions by Kinahan (1857, 1861) are not accurate. They were improved upon by the photographs and drawings of Wollebaek (1908); but unfortunately these are poorly reproduced and, in addition to a hazy dorsal view of the shrimp, include only the first antenna, chela and sixth abdominal segment. A series of drawings of the external features of *C. allmani* has been included to fill this gap (Figs. 12–14). Little need be said in the way of description except that contrary to the account given by Kinahan (1857) there is a well-developed spine on the meropodite of the chela, as in *C. vulgaris*. The differences between *C. vulgaris* and *C. allmani* have been discussed by Wollebaek (1908) and the present study supported his findings.

Although the male pleopods are generally more setose than those of the female, except when the latter is in breeding dress, the only reliable method of sexing *C. allmani* short of dissection is by microscopic examination of the first and second pleopods. In practice the second pleopod was examined. The endopodite of the second pleopod of the male bears an appendix masculina above the base of its inner edge. In the smallest specimens (Fig. 14) the appendix masculina is small and easily overlooked. It is in the form of a small projection from the inner edge of the second segment and bears a single seta at its tip. The appendix increases in size and at maturity has 6 or 7 setae along its inner edge. In the oldest males an additional 6 or 7 setae are attached to the base of the organ. The second pleopod of the female is without an appendix. The endopodite of the first pleopod of the male differs in shape to that of the female (Fig. 14). In the smallest males it is blade shaped with three setae at the tip. As it increases in size the setae become more numerous, 6 or 7 at maturity and many more prior to copulation. It becomes more pointed with age. The endopodite of the female (Fig. 14) is similar in many respects to that of the male, but it is always more elongated and becomes progressively more so with increasing age. Except when the female is in breeding dress there are never more than three short setae present along the inner edge. On assumption of breeding dress the endopodite of the first pleopod, and those of pleopods 2–4, are much modified with numerous ovigerous setae and long pinnate setae. The pattern of ovigerous setae is similar to that described by Yonge (1955) for *C. vulgaris* (Table 6) and the number of these setae varies with the size of the shrimp. The specimen of *C. vulgaris* chosen for comparison in Table 6 is 55 mm long, mature females ranging in size from 45 to 70 mm while *C. allmani* is 37 mm with a range of 26–54 mm.

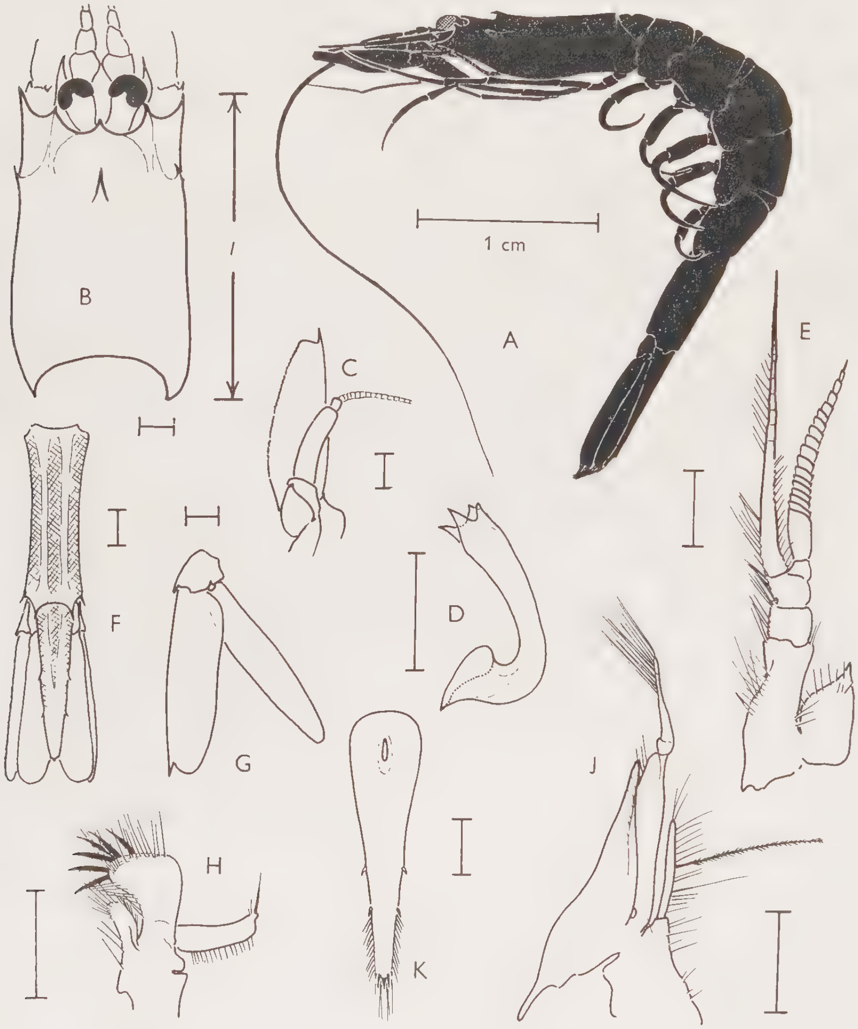

Fig. 12. External morphology of a male *Crangon allmani*. A, lateral view of the animal; B, dorsal view of the carapace with the measurement of length (l) indicated; C, peduncle of the 2nd antenna and its scale, setae not shown; D, mandible; E, 1st antenna; F, dorsal view of the 6th abdominal segment, telson and uropods; G, uropod, setae not shown; H, 1st maxilla; J, 1st maxilliped; K, ventral view of the telson. Except for A, all scales represent 1 mm.

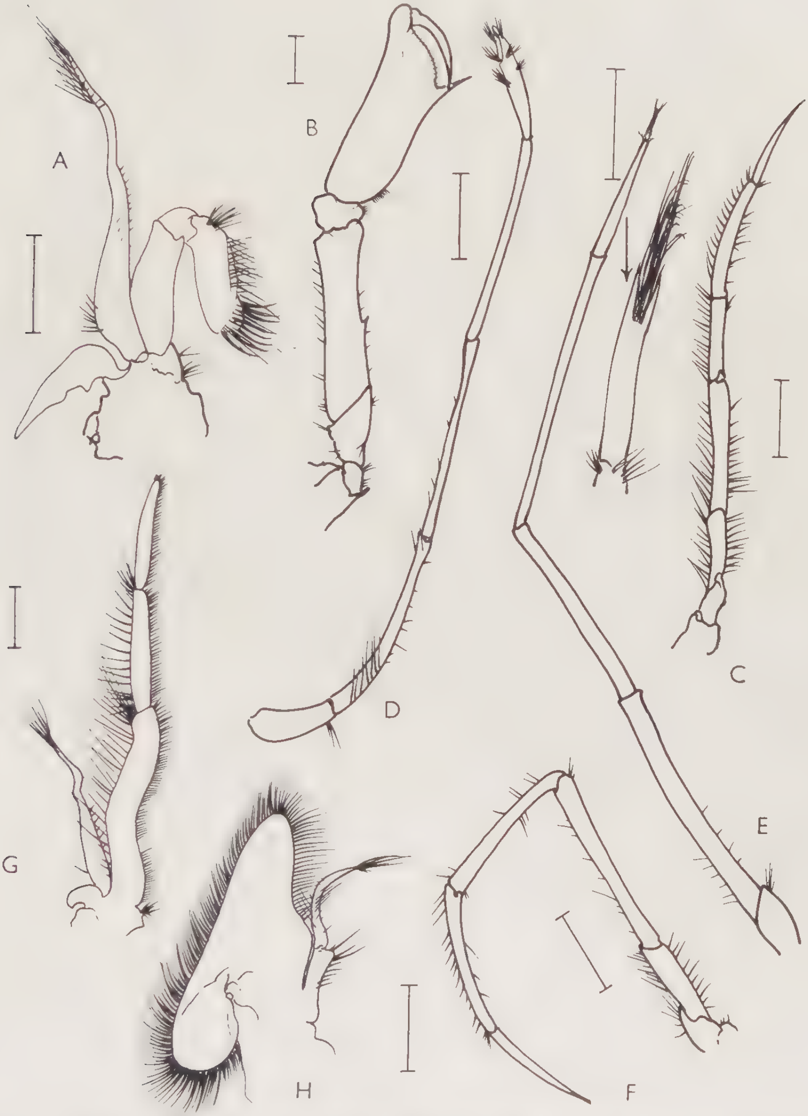

Fig. 13. External morphology of a male *Crangon allmani* continued. A, 2nd maxilliped; B, 1st pereiopod; C, 4th pereiopod; D, 2nd pereiopod; E, 3rd pereiopod; F, 5th pereiopod; G, 3rd maxilliped; H, 2nd maxilla. All scales represent 1 mm.

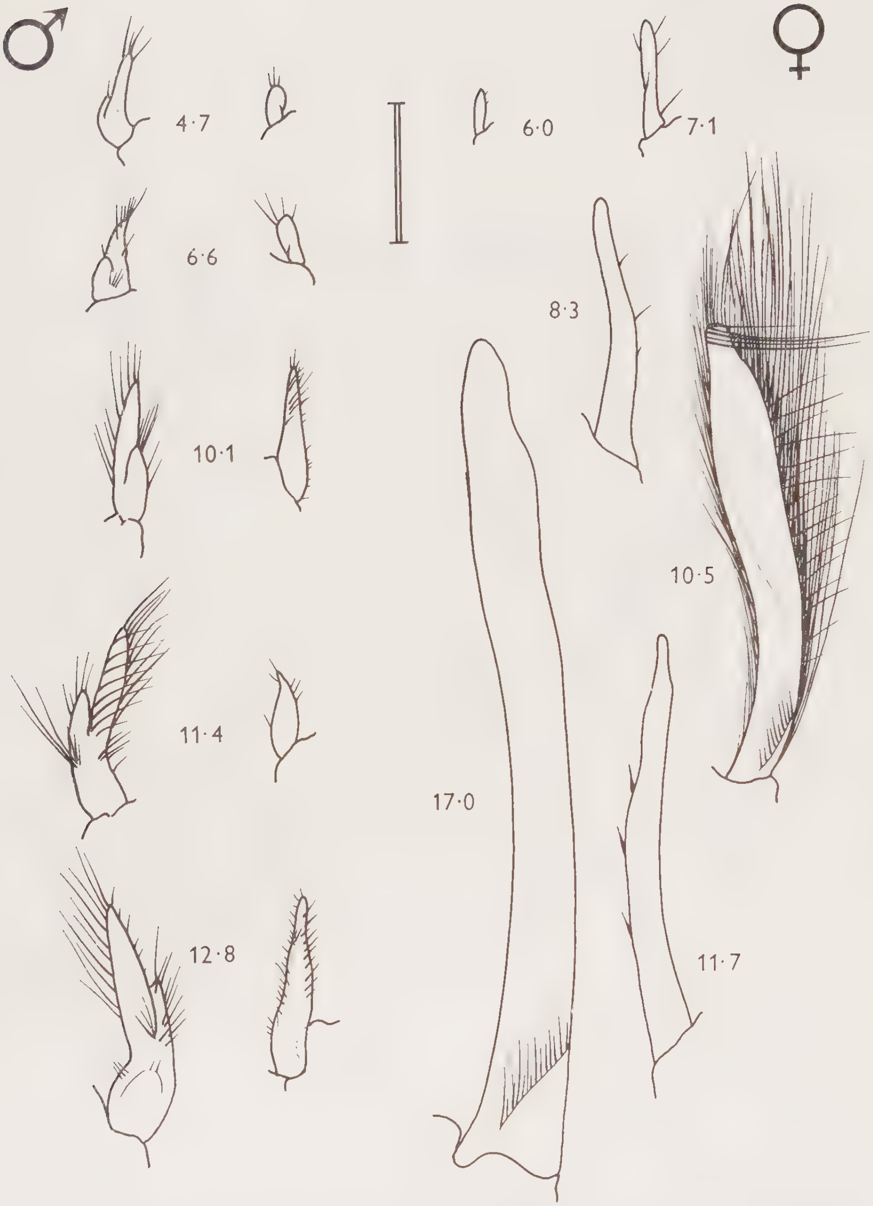

Fig. 14. The development of the endopodite of the 1st and 2nd pleopods of the male and the 1st pleopod of the female *Crangon allmani*. The carapace length of the specimens from which they were taken is indicated at the side of each appendage. The males measuring 10·1 and 12·8 mm have ripe gonads. The females measuring 10·5 and 17·0 mm are in breeding dress, the setae in the latter being omitted. The scale represents 1 mm.

TABLE 6. COMPARISON OF THE NUMBERS OF OVIGEROUS SETAE ON THE PLEOPODS OF *CRANGON VULGARIS* AND *C. ALLMANI* OF COMPARABLE SIZE (SEE TEXT p. 500)

Groups of setae	*C. vulgaris* Pleopods				*C. allmani* Pleopods			
	1	2	3	4	1	2	3	4
C	—	—	—	—	—	—	—	—
Bp	6	5	5	5	5	5	5	2
Bpa	10	3–4	4	2	8–9	5	4	3
Bm	8	8	8	—	6	6	6	—
Bd	5	4	4	—	4	4	4	—
Bda	3	—	—	—	—	—	—	—
E	19–22	—	—	—	21	—	—	—

Data on *C. vulgaris* abstracted from Yonge (1955). The lettering of the groups of ovigerous setae is the same as that used by Yonge (1955). The groups are on the coxopodites (C); the proximal (Bp), middle (Bm) and distal (Bd) regions of the inner margin of the basipodite and also on the anterior face in the proximal (Bpa) and distal (Bda) regions; on the endopodite (E).

DISCUSSION

It would seem that the disappearance of the inshore population during April and May until the following October can be explained by one or more of the following: deep burrowing, mortality, migration.

There is no evidence that the inshore population of *C. allmani* burrows deeper into the substratum during this period. They have not been found by extensive dredging with a variety of methods that sample the substratum to a depth of 10 in. Animals caught in April and kept in the aquarium show no change in burrowing habits. Similarly, there is no evidence for large-scale mortality. It seems possible that early breeding *C. allmani* of carapace length greater than 12·0 mm may die about May but these prawns represent less than 2 % of the total population. Furthermore, the disappearance takes place at the height of the breeding season. Many females bear eggs at stages *a* and *b* at this time and it seems unlikely that these will die before releasing their larvae. By elimination of the other possibilities it seems likely that a migration is the explanation of the disappearance. The North Sea populations of the closely related *C. vulgaris* migrate inshore during May and migration is a feature of the life histories of *Crago francicorum* and *C. nigricauda* (Israel, 1936). Sampling shows that the *Crangon allmani* do not accompany *C. vulgaris* into shallow water nor are they present on the vast areas of rock that are close to the inshore stations. The only area in which *C. allmani* is found in large numbers from May to October is in depths of 40 fm. and over. Further indirect evidence of an offshore migration is that May is the only month in which the inshore and offshore populations have the same average length (see p. 496). Havinga (1929, 1930) and Broekema (1941) show that the largest specimens of *C. vulgaris* tend to remain in deeper water, the smallest specimens migrate first and those furthest inshore are predominantly females. *C. allmani* parallels its relative. Females predominate the inshore population

(Table 7), the average length of the first large inshore samples in November is smaller than those taken later in the inshore period and average length of the offshore samples is higher than those from inshore. It seems a reasonable assumption that the variations in the distribution of *C. allmani* are best explained by an inshore migration in October and an offshore migration in April and May.

TABLE 7. AVERAGE MONTHLY RATIO MALES/FEMALES AT INSHORE STATIONS

Jan.	0·48	July	0·33
Feb.	0·55	Aug.	0·25
Mar.	0·89	Sept.	0·62
Apr.	0·94	Oct.	1·38
May	0·75	Nov.	0·98
June	0·15	Dec.	?

Broekema (1941) finds that the seasonal movements of *C. vulgaris* are related to temperature and salinity. In the case of *C. allmani* the relationship of migration to these two factors is not so clear (see p. 489). Temperature and salinity data of deep water inshore and offshore off the Northumberland coast are given in Fig. 5. From this it is seen that offshore migration coincides with *inshore* minimum temperature. Little can be said of the salinity data except that offshore migration is into water of higher salinity.

Summary of the yearly cycle. In August the *C. allmani* population off Northumberland coast is in deep water (40–50 fm.) 10–15 miles off the coast. This population consists of three main age groups: 0-group, newly metamorphosed shrimps, 1-group, shrimps between 1 and $1\frac{1}{2}$ years most, if not all, have yet to breed and, 2-group, shrimps $2–2\frac{1}{2}$ years that have laid at least two batches of eggs (Fig. 15). In addition there may be a few older female shrimps. During late September and October an inshore migration commences that coincides with the upper temperature limit of the offshore deep water. The smallest 0-group and 1-group shrimps tend to migrate first and although 2-group take part in the migration many remain in deep water. Similarly, some 0-group and 1-group shrimps remain in deep water throughout the year, but the average length of the offshore population is higher than that of the inshore population. The predominance of young shrimps inshore during October to January shown by trawl sampling is confirmed by Goonewardene who in his analysis of the stomach contents of the Whiting (see p. 487) found that he could divide the *C. allmani* into two size-groups, the smaller predominating in the catches from September to January.

During September to December the gonads of 1-group and 2-group mature. The larger shrimps of each group mature first and egg laying commences in the second half of December and continues until the beginning of July. Although a quarter of the mature females lay their eggs in December and January the majority first lay their eggs between March and May. As a second batch of eggs is laid soon after the first hatch, many of the females that bred early in the season will be included in the May breeding population. A third smaller breeding peak in June is probably composed of late spawners with their second brood and, possibly, the largest 0-group females that are a little over a year old. The larvae hatch in 10–12 weeks at the beginning of the breeding season and in 5–6 weeks at the end. Most of the 2-group shrimps have died by the end of the breeding season (August) while newly metamorphosed larvae have joined the population. During April most of the *C. allmani* return to the deeper water, the movement coinciding with the minimum inshore temperature. A few smaller females remain inshore.

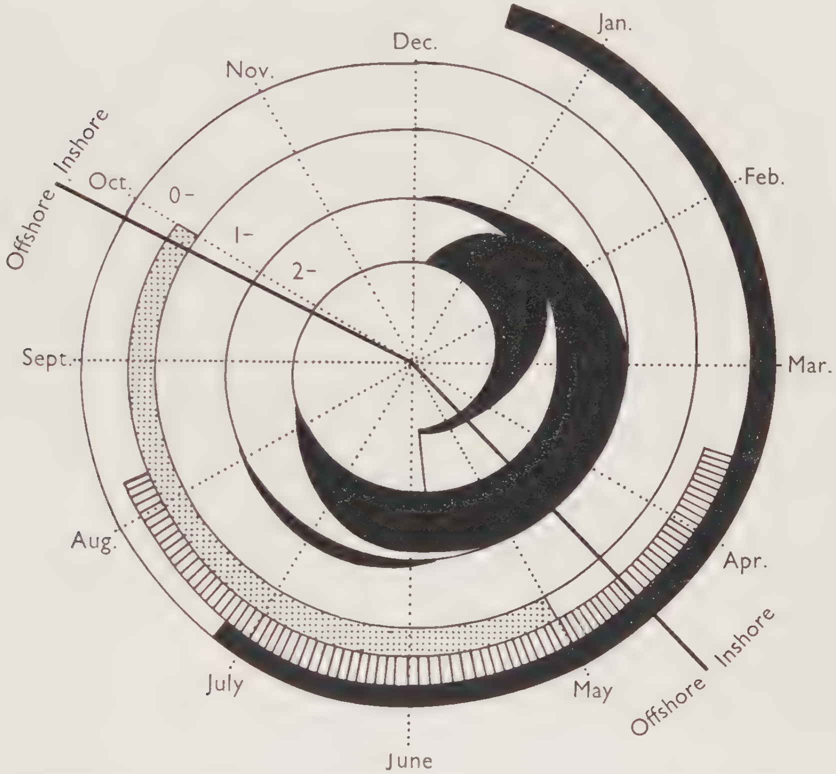

Fig. 15. Diagram representing the life cycle of a year-group. The outer black area is the period when the eggs forming the group were laid. The cross-hatched area is the period when the larvae were released and the dotted area when metamorphosis occurs. The inner black areas represent the period of egg-laying following maturity. The width of these areas gives some indication of the proportion of females with broods.

The life histories of *C. allmani* and *C. vulgaris* are very similar. The most striking difference between the two species is that when *C. vulgaris* migrates* inshore *C. allmani* migrates offshore and vice versa. In the case of *C. vulgaris*, Havinga (1929, 1930), Broekema (1941) and others have shown that salinity, temperature and breeding are significant factors in this migration. While there are differences in temperature and salinity between the deep water at 20 fm. and that at 50 fm. off the Northumberland coast, in comparison with those experienced by *C. vulgaris* these are not very great. Migration of *C. allmani* occurs at temperature maxima and minima and it tends to keep the animal in stable salinity conditions, but the breeding season is not restricted to either the offshore or inshore phase. The differences in the salinity and temperature ranges of inshore and offshore water are so small that it is difficult to visualize what is gained by migration. In the case of *C. vulgaris* rich feeding inshore and stable conditions for breeding offshore seem to be significant. As far as can be seen neither of these conditions apply in the case of *C. allmani*. All this would suggest is that migration in the case of *C. allmani* in Northumberland waters is a relict, possibly inherent, of a movement that was of importance in the past. In fact, it may be that where temperature and salinity conditions are more variable—say in the Kattegat—migration may still be important to *C. allmani*.

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* Meredith (1952) reports that migration does not take place in the population in Liverpool Bay.

TABLE 8. TOTAL NUMBERS OF *CRANGON ALLMANI* TAKEN IN EACH HAUL OF 20 MIN DURATION AT STATIONS 1, 2 AND 3

St. 1		St. 2				St. 3	
18 Nov. 1954	329	4 Aug. 1956	—	6 Nov. 1958	30*	10 July 1956	—
25 Jan. 1955	852	5 Sept. 1956	—	19 Mar. 1959	321	12 Sept. 1956	41
15 Feb. 1955	314	30 Jan. 1957	302	23 Apr. 1959	129	18 Oct. 1956	77
31 Mar. 1955	803	31 Jan. 1957	276	28 May 1959	81	7 Dec. 1956	138
29 Apr. 1955	5	1 Mar. 1957	28	18 June 1959	5	7 Mar. 1957	182
16 May 1955	43	28 Mar. 1957	172	29 June 1959	16	4 Apr. 1957	23
30 Aug. 1955	—	23 July 1957	—	3 July 1959	14	16 Apr. 1957	53
5 Oct. 1955	10	26 Sept. 1942	42	9 July 1959	11	7 June 1957	—
28 Mar. 1956	14	24 Oct. 1957	36	4 Aug. 1959	1	2 July 1957	9
19 Apr. 1956	4	23 Jan. 1958	159	1 Sept. 1959	—	14 July 1957	199
		30 Jan. 1958	193	11 Sept. 1959	—	17 July 1957	3
		21 Feb. 1958	153	25 Sept. 1959	—	30 Aug. 1957	11
		6 Mar. 1958	54	13 Oct. 1959	14	10 Apr. 1958	1
		25 Aug. 1958	4*	10 Nov. 1959	94	22 Sept. 1958	37
						26 May 1959	182
						1 July 1959	224
						11 Aug. 1959	322
						8 Sept. 1959	487
						24 Sept. 1959	118

* Two hauls.

SUMMARY

Since November 1954 the population of *C. allmani* off the Northumberland coast has been sampled at a number of stations.

The collections show that there is a prolonged breeding season from late December to early July. Most females produce at least two broods during each season. The time of development of the eggs of the second brood is half that of the first. Egg numbers vary from 400 to 7000 according to the size of the female and have a diameter of 390 μ throughout the season.

Growth rates and age are difficult to determine, but it is probable that *C. allmani* lives for 3–3½ years with a few females living at least one further year. Males are slightly smaller than the females.

Evidence for migration is discussed. There is an inshore movement in October and an offshore movement in April which appears to be related to temperature.

Examination of the stomach contents shows that *C. allmani* feeds predominantly on *Nephthys* and a variety of small crustacea. There is little difference in diet between inshore and offshore populations.

Details of the external morphology and development of secondary sexual characters are given.

Comparison is made with the life history of the closely related *C. vulgaris*.

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THE IDENTITY OF THE ASCIDIANS *STYELA MAMMICULATA* CARLISLE AND *S. CLAVA* HERDMAN

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(Text-fig. 1)

Carlisle (1954) described *Styela mammiculata*, a new species of stalked ascidian from the Plymouth area, and suggested that it had been brought into British waters, probably with oysters. Its recent discovery on other parts of the south coast of England (Houghton & Millar, 1960) supports the idea that it is an introduced species which is now spreading through a favourable environment. It is well, therefore, to consider whether this may not be a species known from another part of the world. Tokioka (1955) examined one of Carlisle's specimens and suggested that it fell within the range of variation of *S. clava* Herdman. As many specimens of *S. mammiculata* are now available, a more extensive comparison has been made and is reported in this paper.

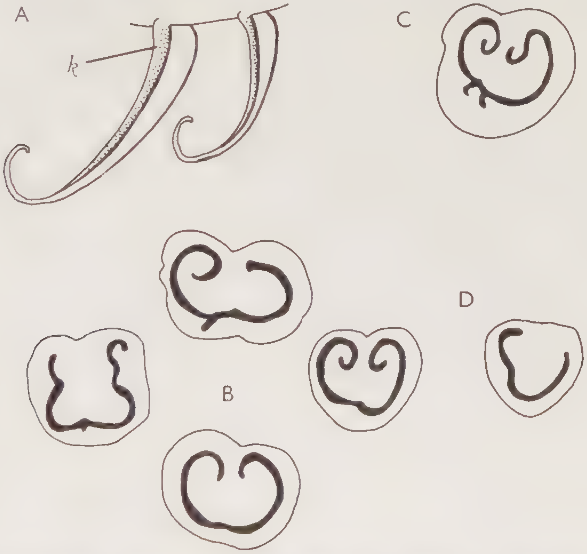

Fig. 1. A, oral tentacles of a specimen from Langston Harbour, to show keel (*k*). B, dorsal tubercles of specimens from Langston Harbour. C, dorsal tubercle of specimen of *S. clava* sent by Dr Tokioka. D, dorsal tubercle of specimen of *S. clava* from the British Museum.

I wish to thank Mr D. R. Houghton for specimens of *S. mammiculata* from Langston Harbour, Hants., Dr T. Tokioka for specimens of *S. clava* and for a translation of his Japanese paper (1955), and the British Museum (Natural History) for the loan of a specimen of *S. clava*.

Herdman's (1882) account of *S. clava* is not very detailed, but has been confirmed and amplified from the only one of Herdman's named specimens in the British Museum which was available for dissection.

TABLE 1. COMPARISON OF *STYELA MAMMICULATA* AND *S. CLAVA*

	S. mammiculata	*S. clava*
No. of oral tentacles	'About 40' (Carlisle, 1954)	'About 30' (Herdman, 1882)
	40, 45, 47, 48, 48, 50, 65, 68 (Langston Harbour specimens)	'More than 45' (Tokioka, 1953)
	33 (Tokioka, 1955)	About 70 (specimen sent by Dr Tokioka)
		About 35 (British Museum specimen)
Branchial bars on right side	D 7 (30) 12 (36) 9 (32) 8 (30) 6	D 1 (39) 4 (37) 5 (40) 5 (34) 3 (Tokioka, 1953)
	D 6 (29) 10 (31) 9 (30) 7 (28) 5 (Carlisle, 1954)	D 4 (36) 4 (35) 5 (42) 5 (20) 6 (specimen sent by Dr Tokioka)
	D 7 (30) 16 (26) 19 (23) 10 (20) 5	D8 (15) 6 (19) 7 (22) 7 (10) 3 (British Museum specimen)
	D 10 (20) 10 (20) 10 (12) 10 (15) 3 D 6 (34) 7 (30) 12 (22) 11 (12) 5 D 2 (32) 6 (30) 5 (34) 12 (36) 3 D 6 (25) 4 (27) 5 (28) 4 (23) 4 D 4 (23) 4 (25) 5 (24) 5 (21) 3 D 9 (20) 7 (22) 6 (24) 4 (20) 5 D 7 (26) 12 (24) 8 (29) 10 (20) 6 (Langston Harbour specimens)	
	D 5 (25+) 6 (28) 5 (25) 8 (17) 5 (Tokioka, 1955)	
No. of gonads	Left: 3 or 4 (possibly 5) Right: 5–7 (Carlisle, 1954)	Left: 3 or 4 Right: 5–8 (Tokioka, 1953)
	Spec. Left Right 1 2 7 2 2 7 3 3 5 4 3 6 5 2 5 6 3 6 7 2 6 (Langston Harbour specimens)	Left: 2 Right: 6 (Specimen sent by Dr Tokioka) Gonads not developed in British Museum specimen

S. mammiculata and *S. clava* cannot be distinguished by external form (Carlisle, 1954, fig. 1; Herdman, 1882, pl. XIX, fig. 9; Tokioka, 1953, pl. LXIV, fig. 6). I find that the oral tentacles of *S. mammiculata*, described by Carlisle as winged, not distinctly keeled, and all of one order of size, are in fact essentially similar in structure, number and arrangement to those of *S. clava* (Fig. 1, A, Table 1). The dorsal tubercle (Fig. 1, B, C, D; Carlisle, 1954, fig. 2E; Tokioka, 1953, pl. LXIV, fig. 9), the arrangement of branchial bars (Table 1), the number, structure and arrangement of the gonads (Table 1) and the form of the gut also fail to separate the species. In the absence of any other distinguishing features I conclude that *S. mammiculata* is a synonym of *S. clava*.

Hitherto *S. clava* has been known only from Japanese waters, the Sea of Okhotsk, and the coasts of Korea and Siberia. Within that area there are places with an annual fluctuation of sea temperature similar to that on the south coast of England. A species surviving accidental transport from the north-west Pacific to the English Channel might spread rapidly under favourable local conditions. This seems to have happened to *S. clava*, the first Japanese ascidian species known to have become established in British waters.

SUMMARY

A comparison of *Styela mammiculata* Carlisle with *S. clava* Herdman shows that they are synonymous. The name *S. clava* has priority.

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ON THE ORGANIC BINDING OF IODINE IN THE TUNIC OF *CIONA INTESTINALIS* L.

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(Text-figs. 1–3)

It is now known that organic binding of iodine takes place in the endostyle of *Ciona* (Barrington, 1957) and *Amphioxus* (Thomas, 1956; Barrington, 1958), and there is evidence that at least di-iodotyrosine and thyroxine are formed as a result of this process in *Ciona* (Barrington, 1959; Robertson, personal communication. Since this biosynthesis appears to be a specialized property of a restricted group of cells, it has been suggested (Barrington, 1959) that it is not a chance by-product of endostylar secretion but that the thyroidal products are a biochemical necessity for the animals concerned. Attention has been drawn also to the occurrence of iodine binding at the surface of the tunic (or test) of *Ciona* (Barrington, 1957), and it is the purpose of the present paper to present some analysis of this latter situation and to enquire as to its possible relationship with the endostylar activity.

The whole of this work has been carried out at Nottingham on animals sent from the Plymouth Laboratory of the Marine Biological Association, and we are indebted to the Supply Department of that Laboratory for the trouble taken in despatching them.

In addition to routine fixation in Bouin's fluid in sea water, followed by staining with the Azan technique, a variety of histochemical procedures have been used. These include chiefly the periodic acid Schiff (PAS) technique, the Millon reaction (Lison, 1953), the coupled tetrazonium technique of Barnard & Danielli (1956 and personal communication), the alcian blue technique (Steedman, 1950; Lison, 1954) the ferric-ferricyanide technique of Chèvremont and Frédéricq (Lison, 1953), and the DDD method for sulphydryl and disulphide groups (Barrnet, 1953; Barrnet & Seligman, 1954).

HISTOLOGICAL AND HISTOCHEMICAL OBSERVATIONS

The ascidian tunic is bounded on the outside by a thin surface layer which it is convenient to term the 'cuticle' (Saint-Hilaire, 1931). Pérès (1948*a*, *b*), whose studies have been of the greatest value to us in formulating our own interpretation, has concluded that this is composed of pure protein, in contrast with the remainder of the tunic which he describes as formed of cellulose (tunicin) with some glycoprotein.

The cuticle (Fig. 1), when well developed, is conspicuous in Azan preparations as a layer which stains sometimes red, sometimes blue, and which shows no obvious structure apart from a thin membrane-like boundary at its upper and lower surfaces. Saint-Hilaire (1931) referred to the fact that many cells with large granules lie near the cuticle and, in his words, appear to adhere to it. In fact, the cuticle (Fig. 1 A) is continued inwards into numerous flask-shaped extensions, each of which encloses one of these cells with its characteristic granule, the latter always staining brilliantly with azocarmine. In this region it is often difficult to decide whether or not the granule is actually still enclosed in a cell, but similar granules are found in wandering cells throughout the tunic; in these the nucleus is clearly defined with the cytoplasm just distinguishable as a very thin bounding layer, and such features are also sometimes visible in the cuticular region (Fig. 1 A). These are clearly the cells which Pérès describes as characterized by possessing a single large 'refringent granule', and we shall therefore use the latter term. According to him they are particularly concerned with the secretion of the cuticle, and our own observations support this view.

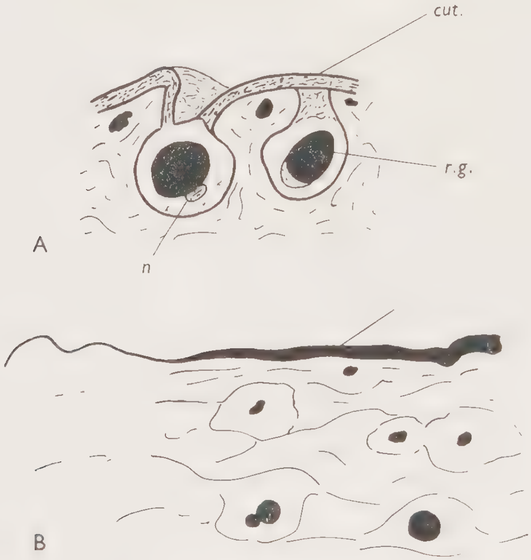

Fig. 1. A. Transverse section of the surface of the tunic of *Ciona*. B. Ditto, showing an early stage in the formation of the cuticle. *cut.*, cuticle; *n.*, nucleus of refringent granule; *r.g.*, refringent granule.

For example, the cuticle varies greatly in development from specimen to specimen. It may appear as no more than a very thin membrane, but in sections of such material (Fig. 1 B) areas can be found where it is becoming much thicker, and at such points there is an accumulation of refringent granules which look as though they are undergoing reduction or fragmentation. It seems evident that these are the source of the increased cuticular deposit, which they resemble in their staining reactions, and that this is why the granules and their cells become enclosed in extensions of the cuticle.

Pérès found that the cuticle and the refringent granules reacted positively to the Millon test, and in confirmation of this we have obtained a definite pink colour in the granules and a fainter one in the surface layer. The reaction has, however, proved rather weak, and we have found the coupled tetrazonium technique of Barnard & Danielli (1956) to give a more precise response, with the added advantage of permanence. With this method, we find that a positive red coloration is given by the refringent granules (more especially at their surface), as also by the cuticle. The remainder of the tunic is predominantly unstained, but the fibres are positive, as are also numerous fine particles, which may perhaps be fibre material. Blocking by benzoylation for 9 h almost completely eliminates this reaction, apart from an occasional weak response at restricted points of the cuticle. We therefore infer that the cuticle and refringent granules include protein, containing tyrosine and perhaps also histidine and tryptophan, and that this is also true of the fibres. Saint-Hilaire (1931) noted the presence of protein in the ascidian tunic, but, using the Millon test, found a good deal of variation between different genera, with a positive reaction from the whole of the tunic of *Halocynthia papillosa*, but none from the tunic of *Tethyum gyrosum*. The significance of such variations is not at present clear, and it will be desirable to investigate them further, particularly in relation to their possible influence upon the degree of iodine binding in different genera.

The results of the alcian blue test are in sharp contrast with the above, for the cuticle and the refringent granules are negative, while the remainder of the tunic, together with the fibres, are positive. This implies that acid mucopolysaccharides are present in the main body of the tunic but are absent from the cuticle and refringent granules, a result which is in agreement with Pérès's description of the former as differing from the latter in staining metachromatically with toluidine blue (presumably gamma metachromasia). He also uses the term 'glycoprotein' in this context, but in current terminology a positive alcian blue response and gamma metachromasia are held to be an indication specifically of acid mucopolysaccharides (Lison, 1953; Pearse, 1954).

With the PAS test, which was not used by Pérès, a positive reaction is given by the cuticle and by the refringent granules; in the rest of the tunic the fibres are positive, and there is a good deal of fine granulation which reacts in the same way, while the general matrix gives a very faint coloration. It seems clear from this response of the cuticle that it cannot be composed of pure protein, as Pérès supposed. Both it and the granules are negative to Sudan black, so that there is no evidence for the presence of lipoidal compounds which might account for the response, and in view of this, and of the absence of acid mucopolysaccharides, it seems likely that the cuticle and granules must consist of protein associated with carbohydrate in some form of glycoprotein complex.

Because of this, and of the recent demonstration by Brunet & Carlisle (1958) of the presence of chitin in the tubes of the Pogonophora, it seemed necessary to re-examine the possibility of chitin being also responsible for the PAS-positive reaction in the cuticle of *Ciona*. For this purpose we have used the standard colour and solubility tests for chitosan as defined by Campbell (1929), using as test material the cuticle of *Ciona*, after removal of as much as possible of the underlying jelly, and comparing the reactions of this with those of *Flustra* (Hyman, 1958) and the cuticle of the locust, and also with samples of bacterial cellulose and of filter-paper.

After treatment for 20 min at 160° C in saturated potassium hydroxide the reactions of *Flustra* and of the locust cuticle were as expected; the material was coloured dark brown on the addition of the iodine solution, on adding 1 % sulphuric acid it became dark blue by reflected light and violet by transmitted light, while on adding 75 % sulphuric acid it became reddish-brown and dissolved. The material also dissolved rapidly in 3 % acetic acid and the solution gave a conspicuous white precipitate on the addition of 1 % sulphuric acid. The *Ciona* cuticle was coloured light brown by the iodine solution, on adding 1 % sulphuric acid it became dark blue by reflected light but blue with a greenish tinge (and definitely not violet) by transmitted light, and on adding 75 % sulphuric acid it became blue and dissolved. It would appear that these reactions must be largely due to the presence of cellulose (tunicin), the presence of this in the tunic being very well-established and readily demonstrable by the Schulze and cuprammonia tests. It is said (Campbell, 1929) that cellulose gives no colour either with the iodine solution or with 1 % sulphuric acid, but we find that while filter-paper and bacterial cellulose, after alkali treatment, certainly give no colour with iodine they can develop a variable degree of blue-black colour on the addition of the acid. Thus the only positive indication of the presence of a substance other than cellulose in the *Ciona* cuticle after alkali treatment is the brown colour reaction which it gives in the presence of the iodine solution; it may be that this indicates the presence of some stable glycoprotein complex, but there is no evidence that it is chitin. This negative conclusion is reinforced by two additional observations. First, the cuticle gives no obvious response to treatment with 3 % acetic acid and no white precipitate can be obtained from the latter by the addition of sulphuric acid. Secondly, Dr S. Wallwork of the Department of Chemistry of this University has been kind enough to carry out an X-ray diffraction study of the cuticle and finds no evidence for the presence of chitin in it. It may be added that earlier workers have obtained negative results from tests for chitin applied to the tunics of *Halocynthia papillosa*

(Saint-Hilaire, 1931) and *Phallusia mammillata* (Saint-Hilaire, 1931; Wester, 1910), and Rudall (1955) found no evidence for its presence in *Rhabdopleura* and the Enteropneusta.

Pérès obtained a positive response from the refringent granules with the Chèvremont and Frédéricq (ferric-ferricyanide) test, and concluded that they perhaps contained sulphydryl groups. We have ourselves obtained with this test a positive response both from the cuticle and the granules, but we have been unable to secure satisfactory blocking in the control preparations. In consequence of this we have preferred to rely upon the more recently developed DDD methods (Barrnett, 1953; Barrnet & Seligman, 1954), and have obtained positive results with them. The procedure for disulphide groups evoked a very faint but definite positive reaction in the cuticle and granules, although the cuticular ingrowths around the latter seem mostly negative. With the procedure for sulphydryl groups a positive response is given by the cuticle, granules and cuticular ingrowths. This reaction, which can be satisfactorily blocked by the method recommended by Barrnet & Seligman (1954), is slightly stronger than that obtained with the disulphide procedure, but the difference is too slight to justify much emphasis. Using the procedure for demonstrating simultaneously both sulphydryl and disulphide groups, with sodium thioglycollate as the reducing agent, a well-defined purple colour is obtained from the cuticle granules and ingrowths, this reaction being decidedly stronger than either of the previous ones. The fibres in the rest of the tunic are very faintly coloured, but it is doubtful whether this could be regarded as a positive response. Slides of sections of the skin of the mouse were processed simultaneously with the tunic sections, and it was apparent that the reactions in the cuticle and granules of the latter, although quite definitely positive, were substantially weaker than those given by regions of relatively high sulphur content such as are found in the stratum corneum and hair follicles of the mouse.

CHROMATOGRAPHY

For the identification of the products of iodination we have made use of radioactive iodine. Animals were immersed for 48 h in sea-water containing 200 μC of ^{131}I per litre, and paper chromatography of the tunics was then carried out according to the procedure of Bowden, Maclagen & Wilkinson (1955), with *tert.*-amyl alcohol 2N ammonia as solvent (Gleason, 1955). Potassium iodide, di-iodotyrosine, tri-iodothyronine and thyroxine were usually added as carriers to the tissue extracts either before distillation or when the drops were placed on the paper, but in some cases a mixture of these was run side by side with the extracts and none was added to the latter. When the run had proceeded sufficiently far the chromatogram was dried and the distribution of the radioactive iodinated compounds recorded by leaving the paper in contact with X-ray film; the latter was developed and fixed and then superimposed on the chromatogram after the distribution on this of the carrier spots had been visualized with the ceric sulphate-arsenious acid reaction (Bowden *et al.*, 1955). Permanent records of these spots were made either by tracing or by ultra-violet exposure.

The material consisted either of the whole tunic, or of the surface layer remaining after as much as possible of the gelatinous tunicin had been removed, and the method of preparing extracts of this for chromatography was varied in the following ways:

(*a*) Material, cut into small pieces, was treated at 37° C for 48 h with buffered trypsin solution. After centrifuging and ether extraction, the supernatant was extracted with butanol/HCl. Chromatography of this extract would reveal iodinated amino acids released by the tryptic hydrolysis of protein present in the tunic, together with any free amino acids.

(*b*) Material, cut into small pieces, was extracted at 4° C for 24 h in saline, a few drops of toluene being added. After centrifuging and ether extraction, the supernatant was extracted with butanol/HCl for chromatography; this would reveal any free iodinated amino acids present in the tunic, together, of course, with any which might have been liberated by autolytic action.

(*c*) The fluid residue left after the butanol/HCl extraction in procedure '*b*' was hydrolysed at 37° C for 48 h by the addition of trypsin solution buffered to pH 8·5, and was then extracted with butanol/HCl. Chromatography of the extract would reveal iodinated amino acids released by hydrolysis of any saline-soluble proteins or polypeptides which were present in the original saline extract.

(*d*) The solid centrifugate from procedure '*b*' was treated with N-NaOH for 5 h at 50° C; after centrifuging and ether extraction, the supernatant was extracted with butanol/HCl. Chromatography of the extract would reveal iodinated amino acids arising from the alkaline hydrolysis of any saline-insoluble protein present in the tunic.

Results

A number of preliminary runs were made with procedure '*a*' in order to standardize the technique, and the resultant chromatograms gave from the beginning clear evidence for the presence of di-iodotyrosine and thyroxine, in addition to iodide. In a series of four definitive runs, each from a different batch of animals, di-iodotyrosine was clearly present in all, while thyroxine was detectible in three (Fig. 2). There was a suggestion also of the presence of tri-iodothyronine, but the separation in this terminal region of the chromatogram was unsatisfactory and the matter needs further study before any conclusion can be drawn. It has been common in our chromatograms for an additional substance to be closely associated with the iodide, and this, too, needs further study.

As regards the saline extracts (procedure '*b*'), a definitive set of three runs (from three separate batches of animals) showed that iodide was clearly demonstrable, as would be expected (Fig. 3). Iodinated amino acids were, however, absent from two, and there was no more than a doubtful trace of di-iodotyrosine in the third. After tryptic hydrolysis of these extracts (procedure '*c*'), iodinated amino acids were still absent from the two mentioned (Fig. 3), while the third showed some di-iodotyrosine and a doubtful trace of thyroxine.

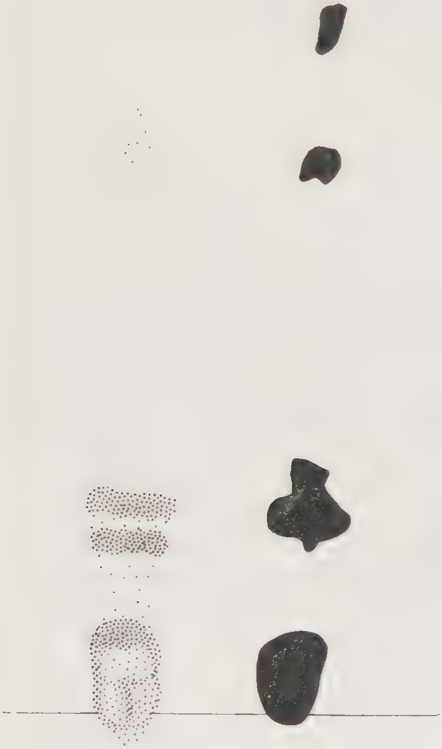

Fig. 2

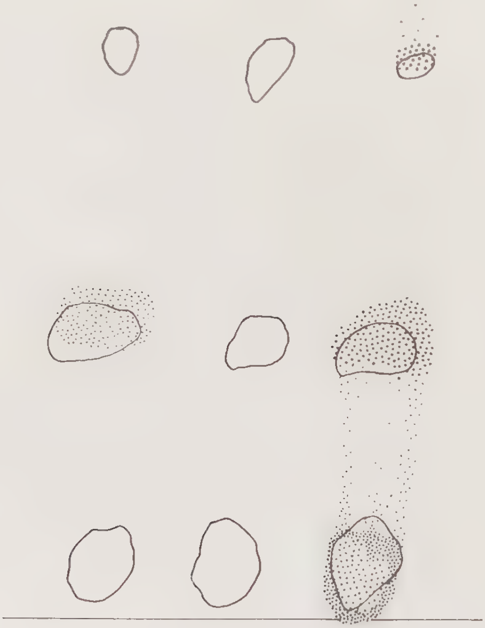

Fig. 3

Fig. 2. Tracings of chromatograms of (to the right) a carrier mixture, showing (reading from the bottom upwards), di-iodotyrosine, iodide, thyroxine and tri-iodothyronine, and (to the left) an extract of the tunic of *Ciona* (procedure '*a*'). Both drops were run in parallel on the same paper. The chromatogram of the carrier mixture was recorded by ultra-violet exposure and that of the tunic by exposure on X-ray film of the sites of radioactive iodine. For further explanation, see text.

Fig. 3. Tracings of chromatograms of extracts of the tunic of *Ciona*, procedure '*b*' to the left, procedure '*c*' in the centre and procedure '*d*' to the right. A drop of carrier mixture was added to each drop on the paper. The sites of radioactive iodine are shown by stippling and of the carrier substances by simple outline (di-iodotyrosine, iodide and thyroxine, reading from the bottom upwards). For further explanation, see text.

By contrast with this, NaOH hydrolysis of the saline-insoluble residue left after these extractions (procedure '*d*') gave clear evidence of the presence of iodide, di-iodotyrosine and thyroxine (Fig. 3), and the last of these seemed a little more readily detectible after this procedure than after tryptic hydrolysis (procedure '*a*'). The tracings shown in Fig. 3 illustrate the results obtained with parallel runs of each of the procedures '*b*', '*c*' and '*d*', using extracts derived from the same batch of material as a starting point. We conclude from the results as a whole that iodine is bound in the surface layer of the tunic mainly to saline-insoluble protein which can be readily hydrolysed, and that the binding involves the iodination of tyrosine residues with the formation of at least di-iodotyrosine and thyroxine.

DISCUSSION

Our observations clearly confirm that the tunic of *Ciona* is covered by a surface layer, or cuticle, which is distinct in composition from the rest of the tunic; it is certainly rich in protein, but this is probably associated with carbohydrate in a glycoprotein complex. The function of this cuticle is presumably protective, and one would expect its protein to be of the general nature of a structural protein. Two categories of such substances are generally recognized, those which are bonded by disulphide groups and those which are quinone-tanned. We have not at this stage any decisive evidence as to the category to which the present protein belongs, but the presence of sulphydryl and disulphide groups suggests that it may be the former.

Quinone tanning demands the presence of a polyphenol and a positive argentaffin reaction is held to give some evidence for this. Using this reaction, we have obtained a dense black response from the refringent granules and a brown colour in the cuticle, the fibres being negative. It is now believed, however, that such a positive response can also be given by tyrosine (Dennell & Malek, 1955), and since this is certainly present it may obviously account for the positive reaction of the cuticle and granules. Moreover, incubation of alcohol-fixed sections of the tunic in freshly prepared catechol solution (Smyth, 1954) has given no evidence for the presence of polyphenol oxidase, while the pale colour of the surface does not in itself suggest that quinone tanning is involved in its formation. While, therefore, a final decision on this point must await the study of a wider range of ascidians, the present evidence certainly favours the view that the surface protein is a keratin-like substance.

Since it appears to follow from the chromatography results that the iodine binding at the surface is associated with this protein, it becomes possible to relate the situation with that which has been noted in many invertebrates. The binding of iodine by scleroproteins has been recorded in a number of groups (Gorbman, 1955; Roche & Michel, 1951). It is certainly true of some of these, and probably of all, that the iodine is bound by the tyrosine residues, for the formation of mono-iodotyrosine and di-iodotyrosine has been clearly demonstrated. Thyroxine can also be formed, and it has been suggested that the yield of this is peculiar to each protein, being determined by the position of its tyrosine residues and the consequent facility for polymerization. In the gorgonids and sponges, for example, where the proteins concerned are pseudo-keratins (Roche & Michel, 1951), only traces of thyroxine have been demonstrated; presumably, therefore, the architecture of the protein molecules of the cuticle of *Ciona* is somewhat more favourable for the formation of this product than is that of the scleroproteins of those groups.

Such considerations bring us to the question as to what relationship, if any, exists between the iodine binding in the cuticle of *Ciona* and that which has been shown (Barrington, 1957) to be associated in the endostyle with a particular group of acid mucopolysaccharide-secreting cells. It may well be, of course, that the co-existence of these two types of iodine binding is entirely fortuitous, but there is another line of thought which bears on this problem. Hecht (1918) has given some reason for supposing that the surface of the tunic is being continuously worn away and replaced. Our observations provide a basis for such a process, for the accumulation of the refringent granules at the surface, and their enclosure by cuticular material, show that continuous deposition of the protein could readily occur. It is worth noting here, incidentally, that according to Roche & Michel (1951) iodination in invertebrate pseudo-keratins occurs most abundantly in the young and rapidly growing parts, so that continued deposition of new protein at the surface of the tunic might well favour the occurrence of iodination there. Now it has been suggested (Barrington, 1959) that the wearing away of the cuticle would result in the release into the water of an iodinated protein which could easily enter the alimentary canal with the food particles carried in by the ciliary currents, particularly since the animals concerned are sedentary and gregarious (while, of course, other ascidian genera are colonial), and that in this way the tunicates might have come to utilize the products of iodination and to have become dependent upon them. Theoretically, this could have been a starting point for the subsequent evolution in the endostyle of a group of cells specialized for the more efficient production of these iodinated products and so, ultimately, for the origin of the thyroid gland as a derivative of that organ.

This argument requires that the animals should be able to digest the protein and so release the iodinated amino acids, and our present results show that this would, in fact, be possible. Scleroproteins are in general thought of as being proteins which are especially resistant to enzymic digestion, but the softer pseudo-keratins are much less resistant than are the hard eukeratins, as much as 25–60 % being dissolved by treatment with pepsin and trypsin (Block & Bolling, 1939). Our chromatographic results show that di-iodotyrosine and thyroxine are readily released from the cuticle by tryptic digestion as well as by treatment with N-NaOH. This suggests that we may here be dealing with a soft pseudo-keratin, although it must be emphasized that information as to the amino-acid composition of the cuticle is necessary before this can be established with any assurance. What is clear, however, is that the protein could be digested under physiological conditions, and that its iodinated residues could be taken up by the animal. Here, then, is a possibility, and at present it is no more than that, of visualizing how the iodination of tyrosine, beginning as a chance by-product of the organization of the surface of the tunic, might have become incorporated into the normal biochemical processes of the tunicates. Even if this possibility is accepted, however, the extension of it to provide an explanation of the origin of the thyroid gland could only be justified if the tunicates are regarded as a basal group from which the vertebrates were derived. Such a view has been widely favoured, but it is not the only one (Bone, 1960), and the matter is raised here primarily because it is at least certain that the facts relating to the distribution of iodine-binding capacity in the Protochordata must be incorporated into any general theory of the origin of vertebrates.

We are greatly indebted to Dr Hamish Robertson, of the Department of Agricultural Chemistry, University of Aberdeen, for guidance in the application of paper chromatography to the identification of thyroidal compounds, and to Dr S. Wallwork, of the Department of Chemistry, University of Nottingham, for carrying out an X-ray diffraction study of the cuticle.

SUMMARY

Organic binding of iodine occurs at the surface of the tunic of *Ciona* with the formation of at least di-iodotyrosine and thyroxine. This process is associated with the presence of a cuticle which is rich in protein, and which contains —SH and S—S groups and probably also some carbohydrate. The protein is largely insoluble in saline, but is readily hydrolysed by trypsin or by N-NaOH with the consequent release of the iodinated amino acids. Attention is drawn to the possible bearing of this situation on the evolution of thyroidal biosynthesis in the Chordata.

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CHEMICAL CHANGES IN SEA WATER OFF PLYMOUTH DURING 1959

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(Text-figs. 1–3)

Analyses of sea water collected during 1959 at the International Hydrographic Station E 1 (lat. 50° 02′ N., long. 4° 22′ W.) are given here in the same form as earlier reports (Armstrong, 1954, 1955, 1957, 1958; Armstrong & Butler, 1959, 1960). The methods of collection and analysis remain the same. Salinities were determined by the Government Chemist, Department of Scientific and Industrial Research. We wish once more to thank Lt.-Cdr. C. A. Hoodless, D.S.C. and the crew of R.V. 'Sarsia', and Capt. W. J. Creese and the crew of R.V. 'Sula' for help at sea.

RESULTS

Temperature and salinity

The vertical distribution of temperature during the year is shown in Fig. 1. The lowest surface temperature was 9·37° C on 10 February; the highest was 18·13° C on 11 August. The surface was appreciably warmer than the bottom in April, and by 12 May a well-marked thermocline at 14 m had developed. It varied between 15 and 23 m in depth during the summer, and vertical mixing was not complete even in October.

Some changes in salinity, suggestive of changes in water mass, occurred in September and October. In August the mean salinity in the water column was 35·07‰ with no significant variation with depth. This changed to 35·11 on 8 September, the increase being accountable to values of 35·19, 35·18 and 35·15 at 0, 5 and 10 m. The mean further increased to 35·19 on 13 October, with values of 35·21 and 35·23 at 50 and 70 m. At the same time mean temperature increased from 14·71 to 15·67° C and silicate decreased from 3·39 to 3·00 μg atom Si/l.

Phosphate

The vertical distribution is shown in Fig. 2, and integral mean concentrations in Table 1. The winter maximum found in January and February was 0·50 μg atom P/l, which is somewhat lower than in the last 3 or 4 years. Consistently low values of 0·08–0·10 μg atom P/l. were found in the upper

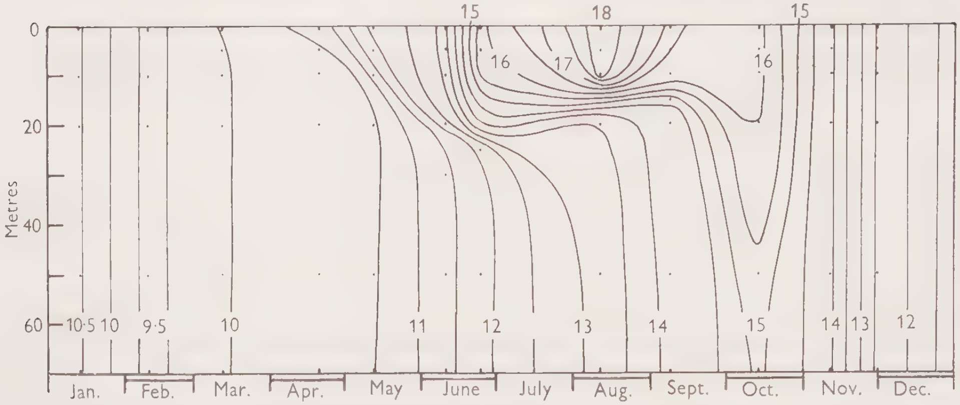

Fig. 1. Vertical temperature distribution at International Hydrographic Station E 1, 1959. Contour lines at 0·5° C intervals.

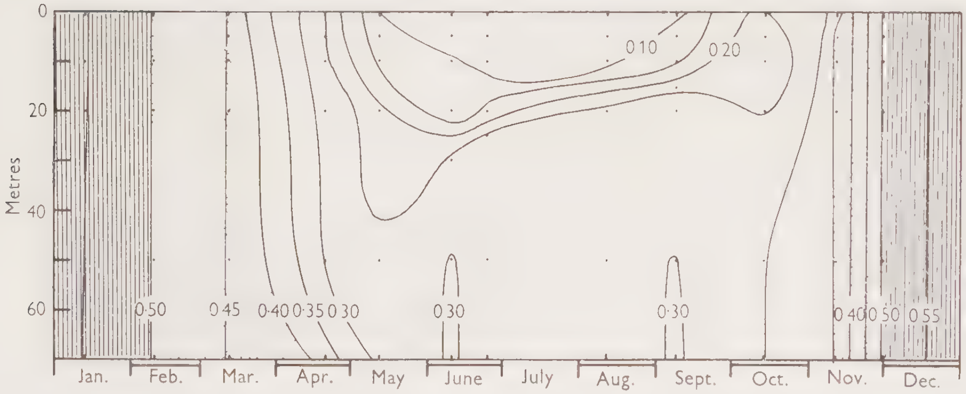

Fig. 2. Vertical distribution of phosphate at International Hydrographic Station E 1, 1959. Contour lines at 0·05 μg atom P/l. intervals.

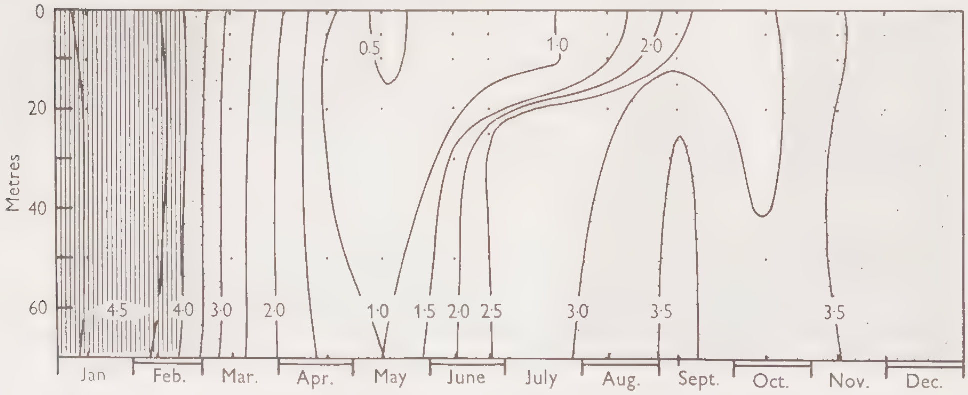

Fig. 3. Vertical distribution of silicate at International Hydrographic Station E 1, 1959. Contour lines at 0·5 μg atom Si/l. intervals.

10 m from May to September. The vertical distribution did not become uniform until 11 November.

Total phosphorus

Determinations made in January, February and March showed the highest values in January. The value 1·36 for the ratio of 'total' to 'inorganic' phosphorus was again unusually high, being the same as in 1958 (Armstrong & Butler, 1959).

Silicate

Vertical distribution is shown in Fig. 3, and integral mean concentrations in Table 1. The winter maximum found was 4·83 μg atom Si/l. in January, and is the highest value recorded since 1950 when the present series of observations started. Silicate had decreased very considerably throughout the water column by 12 May but summer values were not as low as might have been expected, since the summer was unusually sunny. In fact, silicate increased each month during June to September.

TABLE 1. INTEGRAL MEAN CONCENTRATIONS IN WATER COLUMN AT STATION E1, 1959

Date	Phosphate (μg/atom P/l.)	Total P (μg atom P/l.)	Silicate (μg atom Si/l.)
13 Jan.	0·50	0·68	4·83
10 Feb.	0·50	0·63	4·62
12 Mar.	0·45	0·61	2·83
20 Apr.	0·29	—	1·06
12 May	0·22	—	0·68
10 June	0·23	—	1·54
24 June	0·22	—	1·99
11 Aug.	0·23	—	2·67
8 Sept.	0·28	—	3·39
13 Oct.	0·27	—	3·00
11 Nov.	0·36	—	3·59
1 Dec.	0·50	—	3·74

Integral mean concentrations

Some of the values have been discussed. The spring decreases were: phosphate 0·28 μg atom P/l., silicate 4·15 μg/atom Si/l.

SUMMARY

The results of analysis of sea water samples from the International Hydrographic Station E1 during 1959 are given in graphical form and as integral mean values for the water column of 70 m. The winter maximum values were found in January. The spring decreases of nutrients were: phosphate 0·28 μg atom P/l., silicate 4·15 μg atom Si/l.

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STUDIES ON LUMINESCENCE. ON THE SUBOCULAR LIGHT-ORGANS OF STOMIATOID FISHES

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(Text-figs. 1–10)

Many stomiatoid fishes possess a peculiar light-organ below and behind the eye, as well as other kinds of photophores. This light-organ, of diagnostic importance, is termed the subocular, postocular or cheek-organ. Stomiatoid fishes, suborder Stomiatoidei, form a suborder of the Isospondyli. Subocular organs are found in the following groups:

Superfamily Stomiatoidae
  Stomiatidae and Chauliodontidae
Superfamily Astronesthoidae (= Gymnophotodermi)
  Astronesthidae, Melanostomiatidae and Idiacanthidae.

Over the course of the past 8 years I have collected specimens of species belonging to each of the above families, and this material has made possible a comparative study of the subocular organs of the Stomiatoidei.

MATERIALS AND METHODS

Specimens of stomiatoid fishes were obtained from deep-sea catches of the R.R.S. 'Discovery II' and R.V. 'Sarsia'. I am indebted to the Director of the National Institute of Oceanography for the former material. The following species were examined.

Stomiatidae
  Stomias brevibarbatus Ege, 1918. One specimen, 'Discovery' station No. 3354.
  S. ferox Reinhardt (Zugmayer, 1911; Ege, 1918). Four specimens, 'Sarsia' stations No. 7/1957, No. 11 (Kon & Fisher)/1959, No. 15/1959.
Chauliodontidae
  Chauliodus sloani Schneider (Regan & Trewavas, 1929). One specimen, 'Discovery' station No. 3051.
Astronesthidae
  Astronesthes elucens Brauer (Parr, 1927). Two specimens, 'Sarsia' stations Nos. 23/1957, 14/1959.

Astronesthes richardsoni Poey (Parr, 1927). One specimen, 'Sarsia' station No. 12/1959.

Melanostomiatidae

Photostomias guernei Collett (Parr, 1927). One specimen, 'Discovery' station No. 3254.

Idiacanthidae

Idiacanthus fasciola Peters (Parr, 1927). One specimen, 'Discovery' station No. 3354.

Station details

'Discovery' station No. 3051. 26 August 1952. 39° 29′ N., 9° 50′ W. TYF oblique. Estimated depth 700 m.

'Discovery' station No. 3354. See Nicol (1958).

'Sarsia' station No. 23/1957. See Nicol (1958).

'Sarsia' station No. 7/1957. 20 June 1957. 47° 07′ N., 6° 06′ W. Isaacs Kidd trawl oblique. 1800 m of wire out.

'Sarsia' station No. 11 (Kon & Fisher)/1959. 11 October, 1959. 44° 19′ N, 3° 56′ W. Isaacs Kidd trawl oblique. 1800 m. of wire out.

'Sarsia' station No. 12/1959. 9 June 1959. 46° 59′ N., 6° 03′ W. to 47° 01′ N., 6° 00′ W. Isaacs Kidd trawl oblique. 915 m of wire out.

'Sarsia' station No. 14/1959. 10 June 1959. 46° 59′ N., 6° 02′ W. to 46° 57′ N., 6° 03′ W. Isaacs Kidd trawl oblique. 1830 m of wire out.

'Sarsia' station No. 15/1959. 10 June 1959. 46° 47′ N., 6° 03′ W. Isaacs Kidd trawl oblique. 1829 m of wire out.

Treatment

All the stomiatoid fishes listed above were dead when taken from the bucket, or were obtained from preserved collections. They were preserved in formalin and the majority were post-fixed—in Heidenhain's Susa, Bouin's or Zenker's fluids. When necessary, decalcification was carried out with weak formic acid. Embedding media were paraffin wax, polyester wax and celloidin.

Stains used were Ehrlich's haematoxylin and eosin plus Biebrich scarlet; Ehrlich's haematoxylin and eosin plus azure II; a modification of Masson's trichrome consisting of iron haematoxylin, aniline blue and Biebrich scarlet (M 1); a modification of Masson's trichrome consisting of iron haematoxylin, fast green FCF and Biebrich scarlet (M2), iron haematoxylin and orange G; Heidenhain's azan; Holmes's silver.

DESCRIPTIVE HISTOLOGY

In all the stomiatoid fishes examined the suborbital light-organs have the following fundamental plan. A dense mass of photogenic tissue lies underneath the skin. The skin over the light-organ forms a clear window and is separated from the light-organ proper by a narrow space. Investing the back (i.e. the internal surface) of the photogenic mass is an inner tunic or reflector, then a layer of dark pigment. A muscle inserted on the light-organ runs behind and underneath the organ.

The dimensions of the light-organs, and of their component parts, given in the following sections, refer to the specimens which I have examined and are presented merely to give some idea of the degree of magnitude of the structures under consideration. Since deep-sea fish, in illustrations, often seem much larger than they actually are, I have shown the size range of each species, as given in the pertinent literature.

The light-organs of most of the species examined are very similar to each other, the chief exception being *Idiacanthus*. To obviate repetition, the subocular organ of *Astronesthes elucens*, selected as a representative type, is described in detail. Peculiarities and differences encountered in the light-organs of the other species are then presented.

A. elucens Brauer. 146–197 mm. The subocular organ is a small, oval, white structure lying below and behind the eye. On one side of the head of one fish there is a small accessory organ in front of the main subocular organ. External dimensions are 1·5 mm long and 0·8 mm high. The white surfaces of the organs are exposed, i.e. the organs are open in both specimens examined.

The subocular organ proper, i.e. the photogenic mass plus reflector, is beaker-shaped in transverse section (Fig. 1). The outer surface is convex. Dimensions are 0·7 mm high and 0·65 mm deep.

The skin over the light-organ is 10–20μ thick. It consists of a thin epidermis made of stratified squamous epithelial cells, and an underlying dense dermis staining with aniline blue. A space between the dermis and the light-organ ranges from 12 to 100 μ across.

A thin sheath of connective tissue over the outer face of the photogenic mass is 5–10 μ thick. It consists of a dense layer of fibres staining with aniline blue. A little loose connective tissue, also staining faintly with aniline blue, lies over this outer sheath. The outer sheath and loose connective tissue are continuous with loose connective tissue on either side of the light-organ.

The centre of the light-organ is occupied by a mass of glandular photogenic tissue. This is a compact accumulation of cells arranged in cords or circlets. The photocytes are polygonal in section, about 10 μ in diameter, and each contains a central oval nucleus. Around the circumference of the photogenic mass the photocytes appear elongate, with the nucleus in the peripheral half of the cell (i.e. the half of the cell towards the circumference of the photogenic mass). The cytoplasm is granular and stains as follows: M 1, purple (same colour as muscle); eosin and Biebrich scarlet, red; eosin-azure, centre of cell pink, periphery blue; orange G, orange. In photocytes stained with Ehrlich's haematoxylin and eosin, cytoplasmic differentiation appears as follows. Peripheral photocytes have a homogeneous basic cytoplasm, staining blue with haematoxylin below the nucleus. Above the nucleus the cytoplasm is packed with eosinophilic granules. More central cells have a blue peripheral band, tenuous to very broad, about the cell periphery. Within this is red eosinophilic granular material. These apparent differences may result from photocytes being cut at different levels. In this event all photocytes have a homogeneous basiphilic ground cytoplasm, conspicuous at the cell periphery and below the nucleus; the centre of the cell above the nucleus is loaded with acidophilic granules.

The reflector layer, backing the photogenic mass, is 30–60 μ thick. It contains very dense tissue which shines blue by reflected light, and contains some kind of reflecting pigment. By transmitted light the unstained tissue appears light yellow-brown. The reflecting pigment is missing in many sections, dissolved out, perhaps, by some of the staining reagents. The reflecting layer appears to consist of long thin cells. Nuclei are elongate, thin and fusiform. Staining affinities of the tissue are poor: light blue with aniline blue; faint pink with eosin. Blood vessels and at least one nerve penetrate the reflector to supply the photogenic tissue within.

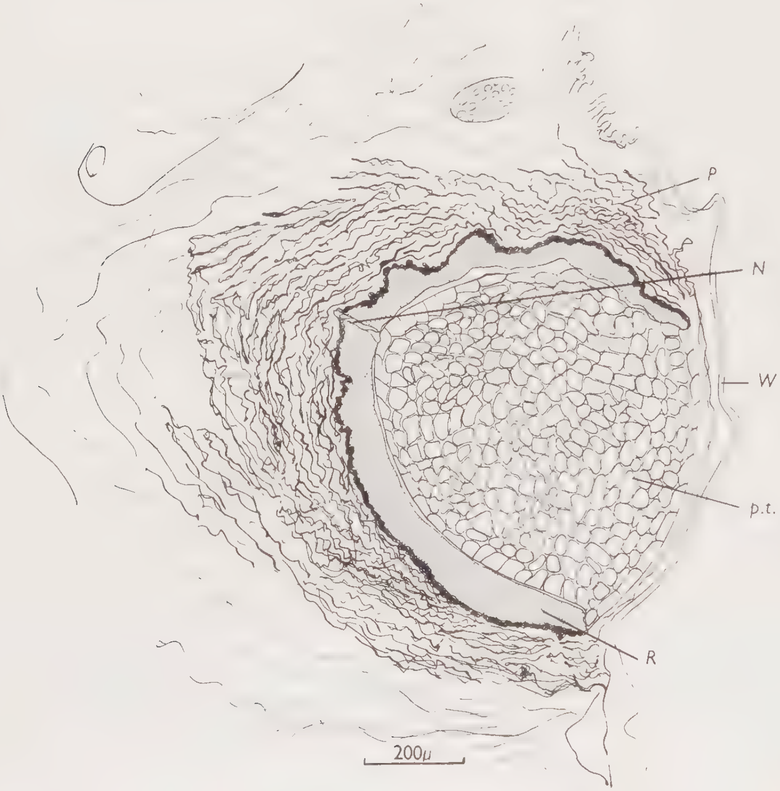

Fig. 1. Transverse vertical section through a subocular light-organ of *Astronesthes elucens*. (*N*, nerve. *P*, pigment. *p.t.*, photogenic tissue. *R*, reflector. *W*, clear window.

Behind (i.e. internal to) the reflector is a wide area of very loose connective tissue containing numerous pigmented cells. These possess dark yellow-brown granules. Some pigmented cells are conspicuously oriented as a unicellular dark sheet immediately behind (internal to) the reflector.

Below the reflector there is a cleft in the pigmented connective tissue, this cleft being continuous with the space in front of the light-organ. There are pigmented cells in the loose connective tissue below the cleft. A long strap-like muscle runs down through the pigmented tissue at the back of the organ, and is inserted in the loose connective tissue underneath the organ, towards the external surface, as described by Brauer (1904, 1908). This muscle passes dorsally, behind the eye, between two sheets of the m. adductor mandibulae, to its origin on the hyomandibula. It is a striated muscle having more slender fibres than the m. adductor mandibulae, from which it is possibly derived.

Astronesthes richardsoni Poey. 150–234 mm. The subocular organs of this fish are rather large, 3·2 mm long and 1·5 mm high. Each organ is oblong in shape and shows as a conspicuous white object against the surrounding skin. In this specimen both organs are exposed, i.e. they are in the 'open' position.

The light-organ proper is lenticular in section, the outer surface being particularly convex (Fig. 2). Dimensions are 1·8 mm high and 1 mm thick. A thin connective tissue sheath covers the outer surface of the photogenic mass.

The photogenic tissue is a dense mass of closely packed glandular cells. These are aggregated into groups, appearing as bands or rosettes in section. They are polyhedral in shape, about 12 μ in size, except at the outer margin of the photogenic mass, described below. The cytoplasm is granular, and generally stains with eosin and orange G. An outer margin or marginal crescent-shaped area of some cells is darker than the centre, and has taken up some haematoxylin.

On the front of the photogenic mass, beginning at the outer margin of the reflector, the photogenic tissue shows another pattern. Externally there is a regular unicellular layer of glandular cells, forming a simple columnar or cuboidal epithelium. The nuclei lie at the outer ends of the cells, against the external surfaces. There is a granular eosinophilic cytoplasm, which stains less intensely in the external region of the cell, and more intensely internally. Inside this layer is a region, one or two cells deep, in which the photocytes appear highly vacuolated, each cell containing a huge vacuole or a poorly staining globular area. With Heidenhain-azan, the outermost cells of the photogenic mass stain blue.

The inner tunic contains reflecting pigment. Nerves and blood vessels penetrate the pigment and reflector layers to invade the photogenic tissue. The muscle to the light-organ is inserted in the connective tissue sheath over the external surface of the photogenic mass.

Stomias brevibarbatus Ege. 39–100 mm (excluding caudal fin). In the specimen available, both subocular organs are rotated equally so that most of the light-emitting surface faces downwards and is concealed; the exposed surface is dark (Fig. 3).

In a transverse section (vertically across the head) the photogenic mass plus tunic is almost circular, 372 μ high and 348 μ deep (Fig. 4). The clear skin over the organ consists of thin stratified squamous epithelium and a little loose connective tissue.

The photocytes are 6–8 μ in size, polygonal, and aggregated into cords or bands. The cytoplasm is dense, granular and acidophilic. No reflecting pigment was observed in the inner tunic. Below the photogenic mass is a cleft or pocket in the connective tissue and underneath the cleft are several layers of pigmented cells.

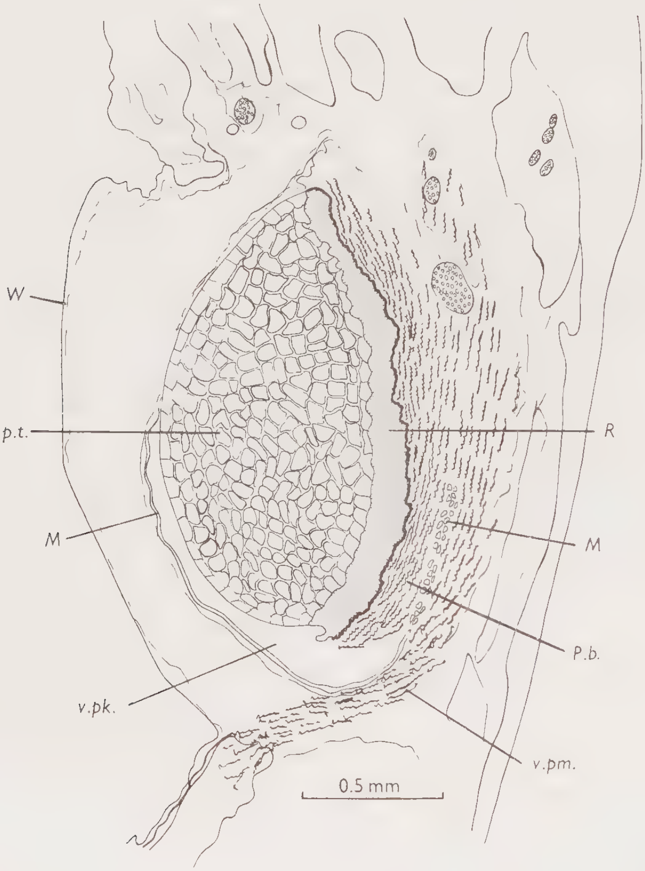

Fig. 2. Transverse vertical section through a subocular light-organ of *Astronesthes richardsoni*. *M*, muscle. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *R*, reflector. *v.pm.* ventral pigment. *v.pk.*, ventral pocket. *W*, clear window.

Stomias ferox Reinhardt. 50–170 mm (exclusive of caudal fin). Four specimens were available, two large and two small. In the two larger specimens the subocular light organs were in the exposed position, i.e. the light-emitting surfaces faced outwards. The organ appeared as a white ovate or pyriform area in a densely pigmented surround. Dimensions were 0·68 mm across and 0·96 mm high, and 0·60 mm across and 0·85 mm high. In the two smaller specimens the subocular light-organs were not visible externally.

In vertical section the photogenic mass is bowl-shaped, with a strongly convex inner, and a slightly convex outer, surface (Fig. 5). Dimensions of the photogenic mass plus pigmented backing are 0·87 mm tall and 0·48 mm thick. Investing the photogenic mass is a thin sheath of connective tissue. The photocytes have a clear ground cytoplasm and contain many small granules, about 1 μ in size, staining with orange G and azocarmine.

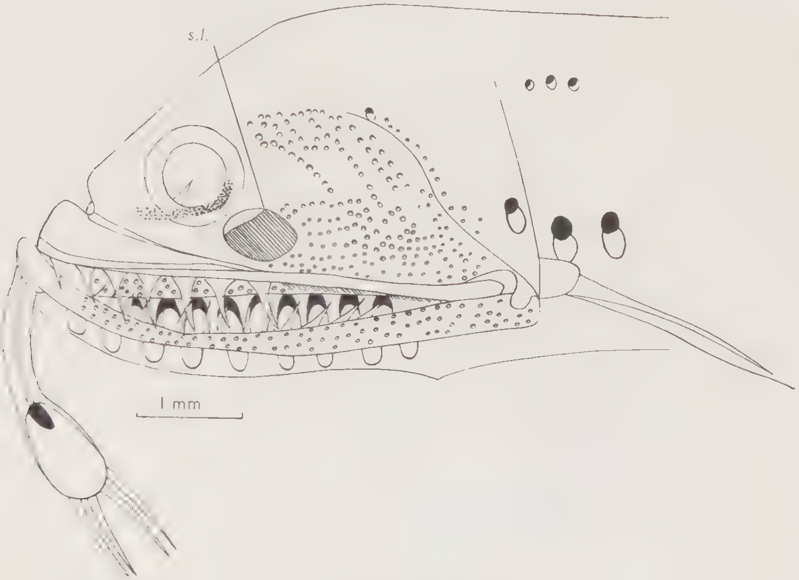

Fig. 3. Head of *Stomias brevibarbatus*. Subocular light-organs (*s.l.*) mostly occluded (rolled downwards.)

Chauliodus sloani Schneider. 20–270 mm (excluding caudal fin). Both subocular organs have the light-emitting surface exposed. Dimensions are 0·38 mm long and 0·29 mm high, including the narrow pigmented surround.

In transverse section, the photogenic organ proper (photogenic mass plus inner tunic and pigmented sheath) is beaker shaped, with a convex outer surface (Fig. 6). It is 384 μ high and 325 μ thick. The photogenic cells are elongate, radiating inwards towards the centre from the margin. They are about 6 μ in diameter, the length is uncertain, perhaps 130–140 μ. The cytoplasm is packed with granular inclusions staining red with Biebrich scarlet.

The internal tunic consists of loosely disposed thin cells, having their longitudinal axes lying parallel to the inner (internal) surface of the photogenic mass. According to Brauer (1904, 1908), this is a reflector layer. Pigment cells form a dense mantle immediately against the light-organ. Beyond this region the pigment cells are arranged more loosely. A ventral screen of pigment cells serves to occlude the emitting surface when the photogenic organ is rotated downwards.

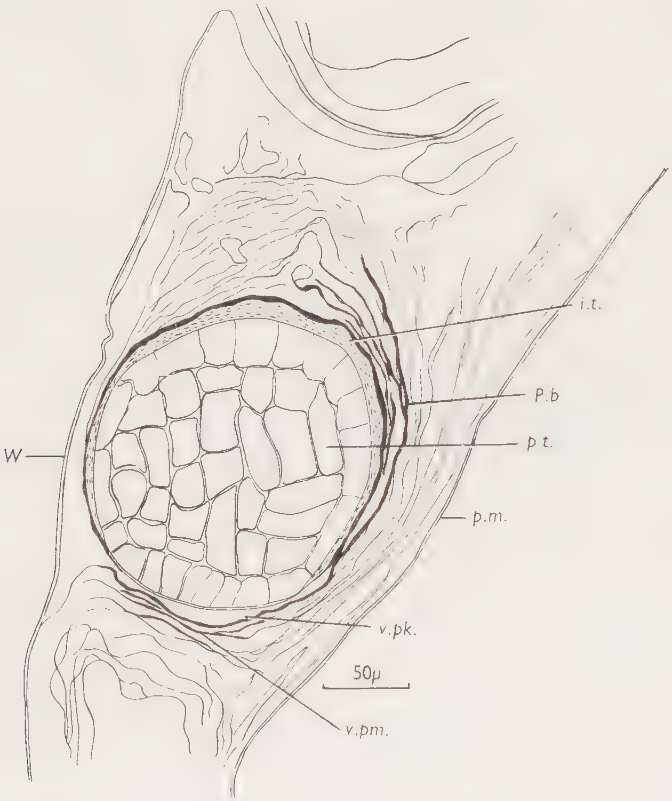

Fig. 4. Transverse vertical section through a subocular light-organ of *Stomias brevibarbatus*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.m.*, pharyngeal mucosa. *p.t.*, photogenic tissue. *v.pm.*, ventral pigment. *v.pk.*, ventral pocket. *W*, clear window.

A band-like muscle, connected to the light-organ, arises dorsally on a long aponeurosis from the hyomandibular bone. The muscle extends ventrally between two sheets of the muscularis adductor mandibulae, then runs through connective tissue obliquely outwards below the light-organ. It is inserted, behind the light-organ, on a long tendon, staining with Light Green (Fig. 7). The tendon runs between pigment cells behind (i.e. internal to) and below the light-organ, and is inserted on the ventro-lateral face of the latter. This muscle-band, serving the light-organ, retains its identity throughout its course; its fibres are striated and smaller than those of the m. adductor mandibulae. It is muscle mm 6 of Tchernavin (1953), who traced it to the dorsal side of the maxillary division of m. add. mandibulae. Tchernavin considered that the photophore-muscle exposed the light-organ, i.e. it rotated it so that the light-emitting surface came to face outwards. This statement

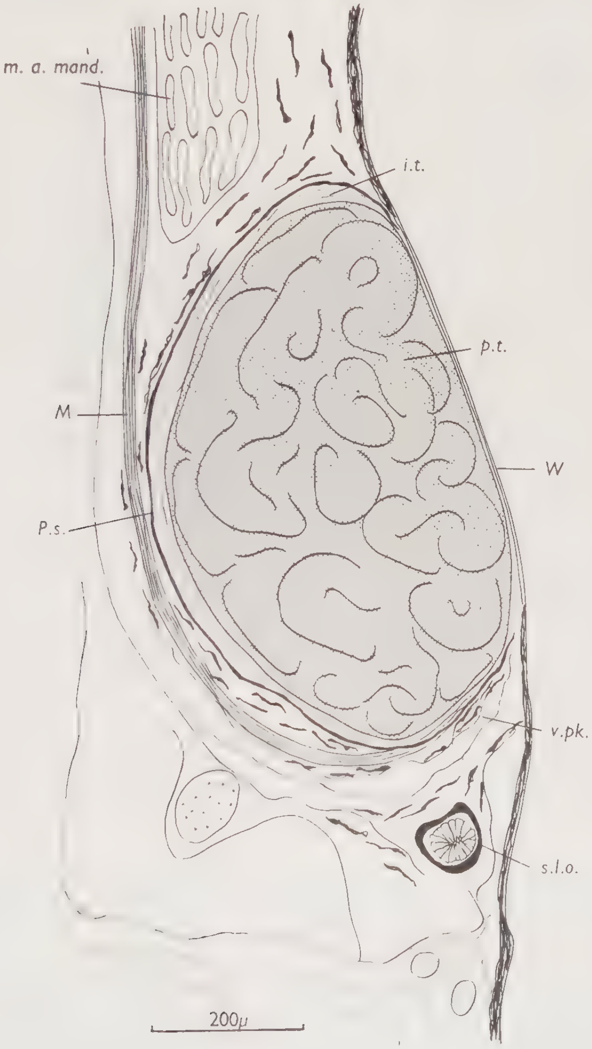

Fig. 5. Transverse vertical section through a subocular light-organ of *Stomias ferox*. *i.t.*, inner tunic. *M*, muscle. *m. a. mand.*, muscularis adductor mandibulae. *P.s.*, pigment sheath. *p.t.*, photogenic tissue. *s.l.o.*, small light-organ. *v.pk.*, ventral pocket. *W*, clear window.

suggests that Tchernavin believed that the muscle was inserted on the dorsal side of the organ. In fact, since the tendon connecting the muscle to the light-organ is inserted on the ventral side of the organ, contraction of the muscle should pull the outer face of the organ downwards, thus occluding the light-emitting surface.

Photostomias guernei Collett. 38–106 mm (excluding caudal fin). The subocular organ is oval-shaped; its dimensions are 0·4 mm high, 0·8 mm long and 0·4 mm thick.

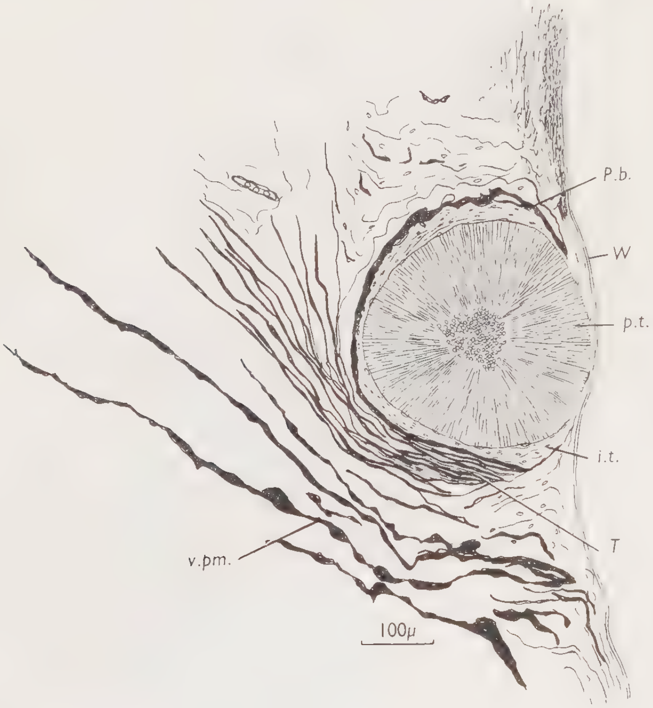

Fig. 6. Transverse vertical section through a subocular light-organ of *Chauliodus sloani*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *v.pm.* ventral pigment. *T*, tendon. *W*, clear window.

The photogenic tissue is about 300 μ thick and has a compact appearance (Figs. 8, 9). The tissue consists of a dense mass of small glandular cells, polygonal in section, each about 10 μ in size. The cytoplasm of a photocyte is finely granular and strongly eosinophilic. The inner tunic contained no reflecting pigment. A muscle is attached to the connective tissue sheath in the ventral region of the photogenic mass. There is a crescent-shaped cleft or gap in the loose connective tissue beneath the light-organ. The depth of this cleft is about equal to the height of the external face of the light-organ. The connective tissue beneath the cleft (and above the mandible) contains black pigment cells.

Idiacanthus fasciola Peters. 80–225 mm (excluding caudal fin). The subocular light-organs are exposed. Each organ is oblong in shape, 0·25 mm long and 0·13 mm high. These dimensions include the pigmented surround.

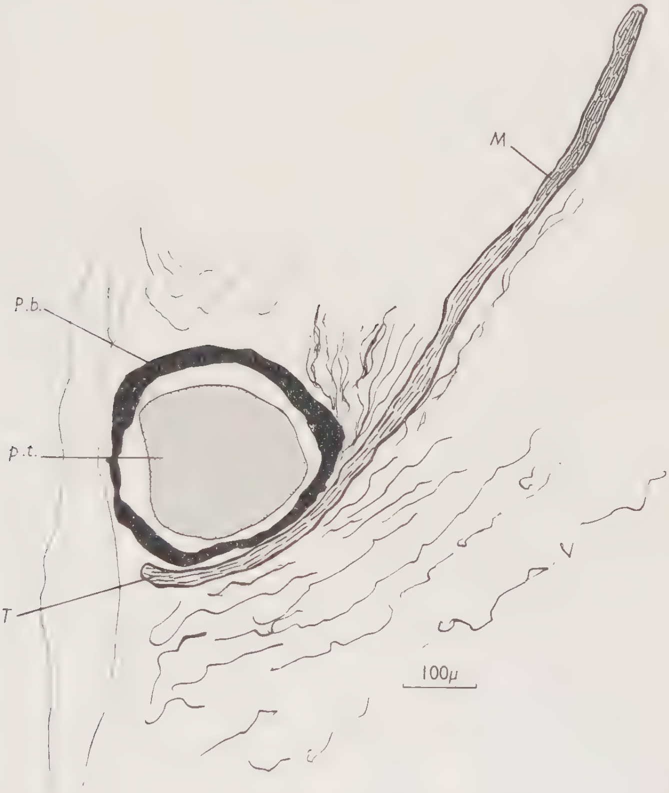

Fig. 7. Transverse vertical section through the head of *Chauliodus sloani*, showing the disposition of tissues in the vicinity of the subocular light-organ. *M*, muscle. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *T*, tendon.

In section the photogenic mass is subspherical, oblate on the outer surface. Dimensions (including pigment tunic) are 96 μ high by 99 μ thick Fig. 10).

The photogenic mass is packed with photocytes. The photocytes are polygonal in shape, 5–9 μ in size. The cytoplasm is granular; the granules are acidophilic, staining with orange G. The internal tunic contains elongate cells having little staining affinity; according to Brauer (1908), this is a reflector layer.

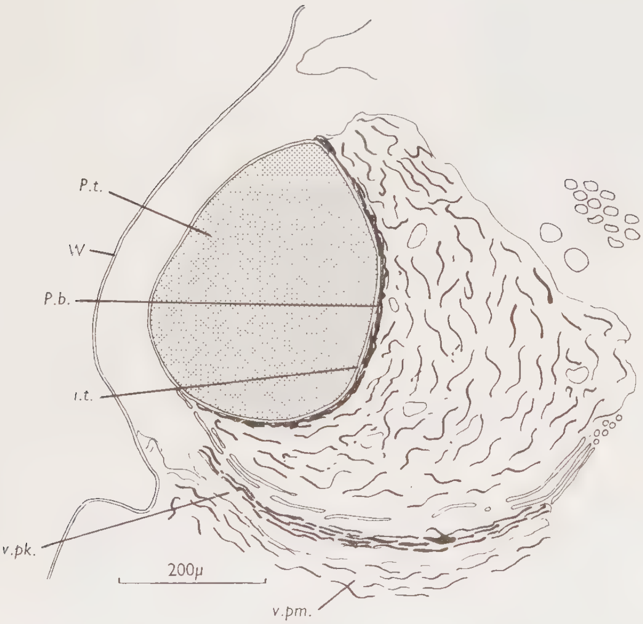

Fig. 8

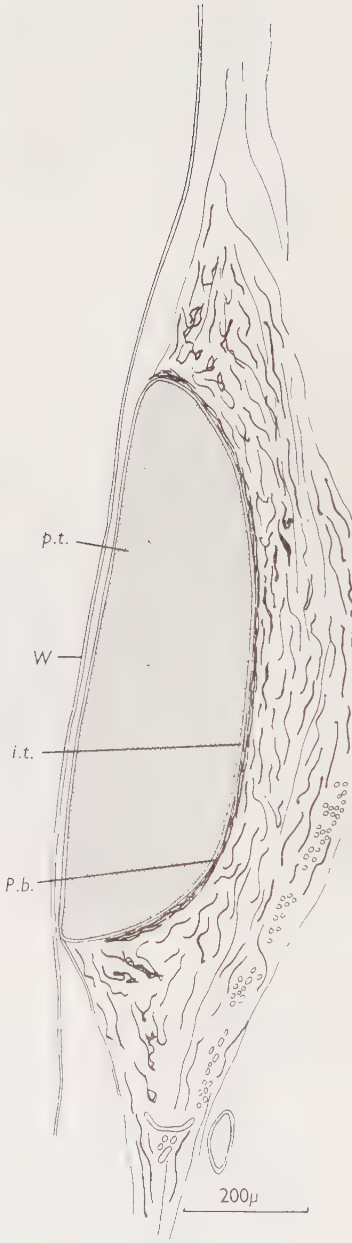

Fig. 9

Fig. 8. Transverse vertical section through a subocular light-organ of *Photostomias guernei*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *v.pk.*, ventral pocket. *W*, clear window.

Fig. 9. Transverse longitudinal section through a subocular light-organ of *Photostomias guernei*. *i.t.*, inner tunic. *P.b.*, pigment backing. *p.t.*, photogenic tissue. *W*, clear window.

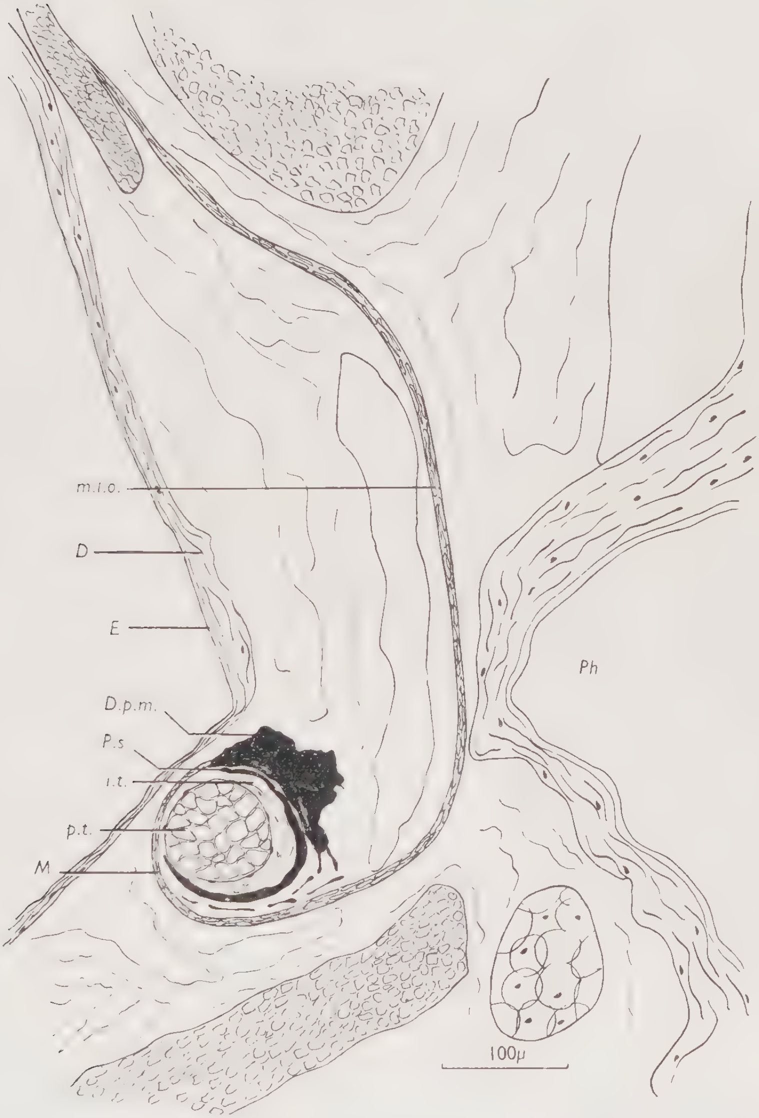

Fig. 10. Transverse vertical section through the head of *Idiacanthus fasciola*, showing the disposition of tissues in the vicinity of the subocular light-organ. *D*, dermis. *D.p.m.* dorsal pigmented mass. *E.*, epidermis. *i.t.*, inner tunic. *M*, muscle. *m.l.o.*, muscle to light-organ. *Ph.*, pharynx. *P.s.*, pigment sheath. *p.t.*, photogenic tissue.

Above the light-organ there is a dense and thick mass of pigmented tissue. A narrow strap-like muscle runs down along the inner surface and below the light-organ, then ascends vertically across the external face of the organ to an insertion in the pigment mass above. This muscle arises from the inner face of the outer sheet of the m. adductor mandibulae. In an illustration of a section through the subocular light-organ of *Idiacanthus*, Brauer (1908) has shown a heavy pigmented mass above the organ. He believed that the muscle serving the light-organ originated on the hyomandibula and terminated on the ventral side of the organ.

There are certain peculiar and significant features in the disposition of the pigment and the course of the muscle band in *Idiacanthus*, which differ from those obtaining in the other stomiatoids described in this paper. The pigment mass that could be concerned with screening off the light lies above the light-organ, not below as in the other species. The muscle to the light-organ is not inserted on its ventral surface, but passes right around the organ to terminate on the dorsal pigment mass. It would seem that the only way these structures could operate so as to screen off the light would be for the muscle to pull down the dorsal pigment mass over the front of the light-organ, like a shutter.

DISCUSSION AND CONCLUSIONS

The subocular light-organs of all the stomiatoids examined conform to a common pattern. There is usually one fairly conspicuous organ below and behind each eye. The organ is rather simple in structure, consisting of a mass of photocytes, backed by a feebly staining inner tunic and a screen of melanophores.

Reflecting pigment has been recognized in the inner tunic of some species (*Chauliodus*, *Astronesthes*, etc.). It may always be present, and be lost in some instances during preservation and subsequent histological treatment. Brauer (1904, 1908) has termed the inner tunic the reflector layer. The nature of the reflecting pigment in the light-organs of teleosts is not known (Nicol, 1957). The identification of the pigment is of interest because its absorptive and reflecting properties can be interpreted in terms of the spectral composition of the luminescence, and the role it plays in the photophore will be better understood.

Usually the photocytes are alike, and there is much similarity in the photogenic tissue of different species. They are small cells, sometimes possessing a strongly basophilic cytoplasm, and they are packed with acidophilic granules. In one species, viz. *Astronesthes richardsoni*, cytological differentiation within the photogenic tissue is recognizable.

There is no lens system for focusing the light, nor for enlarging the apparent size of the source. When a reflector is present, it is possible that it acts to some extent as a parabolic mirror.

A muscle goes to each light-organ. It arises from the hyomandibula, or from the muscularis adductor mandibulae, and runs down behind the eye inside and below the light-organ. It is usually inserted in the connective tissue sheath on the outer surface or ventro-lateral surface of the photogenic mass. In *Chauliodus* the muscle arises from an aponeurosis attached to the hyomandibula, and is inserted on a tendon which goes to the ventral surface of the light-organ. Its action appears to be the same as in the other species in which the muscle extends over the entire path from hyomandibula to light-organ. From the manner in which this muscle is arranged it is probable that it pulls the outer face of the light-organ downwards. Brauer (1904, 1908) recognized this muscle in a number of different stomiatoids (*Chauliodus*, *Astronesthes*, etc.), and he also believed that it rotated the light organ ventrally. Since there is a black pigmented layer in the connective tissue below the light-organ, this action serves to screen the light-emitting surface.

Idiacanthus is peculiar in that a pigment layer lies above the light-organ, and the muscle passes upwards, in front of (i.e. external to) the light-organ, to be inserted in this pigment layer. It seems that the muscle pulls the pigment down in front of the light-organ of *Idiacanthus* and does not move the photogenic mass.

Confirming Tchernavin (1953), I have found no antagonist to the muscle mentioned above. It is not apparent how the light-organ (or shutter in the case of *Idiacanthus*) is rotated to a position so that the light-emitting surface is exposed. Suggestions awaiting confirmation are that the muscle works against elasticity of connective tissue, or that some displacement of fluid is involved, and raised hydrostatic pressure moves the light-organ back into the exposed position when muscle traction is released.

The light-organ muscle appears to originate anatomically in some instances from the maxillary division of the m. adductor mandibulae, and it may be derived ontogenetically from the latter (cf. Tchernavin, 1953). In this event, its innervation may be ascribed to the trigeminal nerve which supplies the m. add. mandibulae (cf. Allis, 1897). Apart from this muscle-innervation, the light organ is supplied directly by nerves which penetrate the enveloping tunics and sheaths to reach the photogenic tissue. I have identified these nerves in *Astronesthes* and Brauer (1904, 1908) observed nerves in the subocular light-organs of other stomiatoids. The origin of these nerves has still to be traced.

Examining young stomiatoids, Brauer (1904, 1908) observed a lumen in the photogenic mass. In adults the photogenic tissue appears to be made up of convoluted cords of photocytes. Brauer suggested that this tissue is formed by invagination of surface epithelium, which then proliferates. Support is given to this hypothesis by the observations of Greene (1899), who actually found a process of this kind taking place in the development of skin photophores in the midshipman *Porichthys*.

Living stomiatoids have been seen luminescing by a few observers. Haneda (1955) stated that the subocular light-organ of *Astronesthes ijimai* luminesces continuously, and that the luminous surface appears and disappears by rotating the organ. He suggests that luminous bacteria may be present, but in conversation recently he has discounted this idea. There is no doubt, from histological examination, that luminescence is autogenous, not bacterial.

Specimens of living *Echiostoma* have been observed to luminesce. Harvey (1931) found that the cheek organ, partially pink in life, flashed with a blue luminescence when the fish was handled. Following the injection of adrenaline, yellowish luminescence appeared in the photophores near the point of injection and soon spread to most of the other photophores. No luminescence appeared in the barbel. The cheek (subocular) organ continued to flash at intervals after the injection of adrenaline, but its rhythm and brightness were unaltered. Harvey asserted that the light appeared and disappeared in the subocular organ itself; the flashing was not due to unscreening of a continuously luminous surface. Beebe & Crane (1939) have written that 'The postorbital is definitely under control of the fish, can be rolled down out of sight, and made to glow steadily or emit sharp flashes', and 'In the new *Tactostoma*..., it apparently rotates forward and downward, instead of the usual downward'. Melanostomiatoids were observed from the 'Bathysphere' by Beebe (1935). The lateral serial organs usually glowed steadily; cheek organs, occasionally blinked and were rolled 'down' into sight.

In *Chauliodus sloani*, a weak continuous blue light has been observed on the ventral surface; the intensity of this light was not increased by mechanical stimulation. Following mechanical stimulation the serially arranged photophores luminesced, the response beginning near the point stimulated and spreading along the length of the fish; after a few seconds the light faded (Grassi, n.d.; Skowron, 1928).

Beebe (1935) has also observed luminescence in the barbel of various stomiatoids, and I found that the barbel of *Leptostomias* lighted momentarily after mechanical stimulation (Nicol, 1958).

The behaviour of a living stomiatoid (species unknown) under natural conditions has been reported by Clarke (1950). The fish was observed near the surface from the deck of a ship near the South Sandwich Islands. The stomiatoid fish, about 25 cm long, emitted a beam of varying intensity which shone directly forwards for a distance of about 0·6 m. The fish was lurking 0·6–1·8 m below the surface, poised at an angle of 35–40° from the horizontal, in which position the beam had an upward tilt. Occasionally, the fish swam around and with a quick action snapped at a cloud of krill above it.

Some miscellaneous references to luminescence in stomiatoids are given by Brauer (1908). These accounts do not clearly distinguish between the several kinds of light-organs.

From the view point of functional anatomy some tentative conclusions may be induced from the miscellaneous observations now available dealing with the subocular light-organs of stomiatoids. Light-production is intracellular and autogenous; this follows from the histological evidence, and from Harvey's observation (1931). Luminescence is subject to direct nervous control; evidence includes periodic flashing and innervation of photocytes. The organ also can be rotated so that the light-emitting surface is hidden. Haneda (1955) states that this is a way of extinguishing the light. Mechanical screening, then, forms a second method of regulating emission. It may be that direct nervous action is concerned with protracted emission; rotation, with brief periodicity. An analogous situation is encountered in squids which have photophores provided with screens of chromatophores. The photophores are innervated directly and the chromatophores, by expansion and contraction, occlude and expose the luminous surface of the photophore. The surface of the subocular light-organ is white or coloured, reflecting and conspicuous against the black background of the head, and rotation provides a means of hiding this salient feature.

In all specimens in which the subocular light-organs were partly or wholly occluded, both organs in the fish were rotated to the same extent. It seems fairly certain that both members of the pair are operated in unison.

Luminescence appeared in the submental barbel of *Leptostomias* and in the subocular organ of *Echiostoma* after mechanical stimulation; in neither animal were the other photophores affected. Continuous light has been observed in the multitudinous small (simple) photophores of the outer corium of *Chauliodus*; the serial photophores lit up when the fish was stimulated mechanically. Beebe found that the injection of adrenaline induced luminescence in the serial photophores of *Echiostoma* without affecting other light organs.

Elsewhere, I have suggested (Nicol, 1957) that the serial photophores of teleosts are controlled by adrenergic nerve fibres of the sympathetic nervous system. When excited, the photophores of this system appear to respond as a unit. Since the other photophores of the head (viz. subocular, barbel) are not necessarily called into action at the same times, it is likely that their respective innervations are from a different source; indeed, the innervations of barbel and subocular light-organs may themselves be dissimilar from each other.

I would suggest that the dissimilar kinds of light-organs plus their different innervations signify that they are employed in several different ways. Stomiatoids are carnivores living below the level of effective light-penetration; some species are reported to come to the surface at night to feed (Beebe, 1926; Clarke, 1950). To judge from the frequency with which they are captured in nets, they are solitary hunters. In the dark depths where they live, much of the light needed for vision they must generate themselves. In shallow waters, in the neritic zone and in upper pelagic reaches, some fishes possess attractively shaped, coloured or actuated lures. In these regions, fishes make use of concealing coloration and warning coloration; males and females sometimes have dissimilar colour patterns concerned with occupation of territory and mating; some fishes advertise by suddenly exhibiting conspicuous fin-patches, etc. With these chromatic features are linked special behavioural characteristics. By analogy we might expect to find many of these roles, and perhaps others as well, performed by the light-organs of deep-sea fishes.

Bulbs on submental and dorsal tentacles may be fishing lures; this suggestion derives from analogy with the fishing tentacles of surface or neritic antennariids and lophiids, and the escal bulbs of deep-water Pediculati. The large subocular organs may be used as torches, for illuminating the surrounding water. The serially arranged photophores may permit the animals to recognize each other. The result may be mutual repulsion, thus keeping the fish spread out in hunting territories delimited by the intensity of the light and the distance at which it can be seen; or mutual attraction when the animals differ in sex. Possibly the same light-organs are used for different purposes; there may be patterns of signals and response, just as there are among inshore fishes, that allow the sexes to be distinguished. Although these problems seem rather intangible, there is a fair possibility that answers to them can be secured by various lines of attack, as the opportunities arise.

I would thank Mr A. C. G. Best for help with histological preparations.

SUMMARY

A histological study of the subocular light-organs of the following stomiatoid fishes has been carried out, viz. *Stomias brevibarbatus*, *S. ferox*, *Chauliodus sloani*, *Astronesthes elucens*, *A. richardsoni*, *Photostomias guernei* and *Idiacanthus fasciola.*

The subocular light-organ is a fairly large photophore lying just behind and below the eye. In all the species examined, except the last, it consists of a subspherical or elongate mass of photocytes, backed by an inner tunic and black pigment sheath. This assemblage, the light-organ proper, lies in the corium. The inner tunic sometimes contains reflecting material.

The photocytes are small polygonal cells, sometimes elongate and radiating outwards from the centre of the photogenic mass. They contain abundant acidophilic granules. In some species the ground cytoplasm is strongly basophilic.

The skin forms a clear window over the light-organ. There is a space between the dermis and the external face of the light-organ proper. Beneath the light-organ there is another layer of pigmented cells. A nerve penetrates the back of the light-organ to reach the photogenic tissue.

A long strap-like muscle, arising from the hyomandibula, runs down inside and beneath the light-organ to an insertion on the ventro-lateral or external

face of the light-organ (except *Idiacanthus*). The function of this muscle is to pull the outer face of the light-organ downwards, in which position the light-emitting surface faces the ventral pigmented layer and is occluded.

In *Idiacanthus* the light-organ proper is similar. A pigmented layer lies above the light-organ, and the muscle passes underneath and across the external surface of the photogenic mass, to be inserted in the dorsal pigmented layer. The muscle pulls the dorsal pigmented layer down in front of the light-organ, like a screen.

From observations on the histology of the light-organs, and on living fish, some conclusions are drawn. Luminescence is autogenous and is subject to direct nervous control. In addition luminescence can be cut off by rotating the light-organ (or by pulling down the shutter in *Idiacanthus*). This action also conceals a conspicuous reflecting surface, apart from affecting luminescence. Control of the several kinds of light-organs of stomiatoids appears to be independent of each other, viz. regulation of tentacle bulb, subocular organs, and serial photophores, seemingly by different parts of the nervous system.

Suggested roles of luminescence are discussed.

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A CONTRIBUTION TO THE BIOLOGY OF *ASTRORHIZA LIMICOLA* (FORAMINIFERA)

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(Text-figs. 1–5)

In the last few years the exceptionally large monothalamous arenaceous rhizopod, *Astrorhiza limicola* Sandahl, 1858, has been collected in appreciable numbers from the Blyth and Plymouth areas of British coastal waters. These collections of the living animals have enabled the authors, both independently and jointly, to make certain observations of the behaviour of the animal, and of the structure of the test, which have not been appreciated hitherto. With the exception of two early accounts of *A. limicola*, one by Bessels (1875) under the name *Haeckelina gigantea* and the other by Schultz (1915), very little appears to be known of the biology of any member of the family Astrorhizidae.

DISTRIBUTION

Astrorhiza limicola, the type species of the genus *Astrorhiza*, was first described from specimens collected off the Bolus coast, Skagerak (Sandahl, 1858) and recent faunistic accounts by Högland (1947) and Christiansen (1958) indicate that it is well established in the sandy-mud sediments in shallow water (12–58 m) of the Kattegat, Skagerak, the Gullmar and Oslo Fjords (Dröbak Sound). The numerous records of the animal in British coastal areas are all from sand, sandy-mud, or miry sediments at depths ranging from 20 to 130 m (Brady, 1884, 1887; Robertson, 1901; Heron-Allen and Earland, 1909; Stephen, 1923; Plymouth Marine Fauna, 1957). This apparently consistent occurrence in shallow waters, also noted by Cushman (1918) who lists early records from the North Atlantic coast of America, is upset by two old yet often neglected records, one by Carpenter & Wyville Thomson (1868) from a station due north of the Hebrides at 59° 36′ N. 7° 20′ W. and the other by Norman (*teste* Jeffreys, 1876) in the Davis Strait at 59° 10′ N. 50° 25′ W., where the depths are 970 and 3200 m, respectively. Although the specimens do not appear to be available for examination, the short descriptive accounts indicate that the records are justified, so that the depth range of the species has to be extended beyond that which it is customary to acknowledge.

Apart from the North Atlantic, records from the Arctic north of the New Siberian Islands (Stschedrina, 1946) of *A. limicola* var. *arenifera* and *A. limicola* var. *sabulifera* are of interest, although in a recent private communication Mrs Stschedrina has informed one of us that she is revising her opinion about the systematic position of these forms. The only reports of *A. limicola* from the southern hemisphere are those from the east coast of Africa (Heron-Allen & Earland, 1915), the Antarctic (Heron-Allen & Earland, 1922) and South Georgia (Earland, 1934) all of which are based on either fragments or odd specimens. Re-examination of this material from the southern hemisphere has led to the conclusion that these records should be provisionally considered as doubtful.

QUANTITATIVE DATA AND THE NATURE OF THE ENVIRONMENT

The distribution of *A. limicola* has been most fully studied on the offshore grounds of the southern half of the Northumberland coast. All along this coast there is a strip of muddy sand from 8 to 10 miles wide at depths from 30 to 70 m running parallel to the coastline. Farther offshore the bottom falls off to depths of 80–100 m where the sediments are predominantly sandy silt. At a distance of 20–25 miles offshore the bottom rises once again to depths of 60–70 m and muddy sand sediments are again encountered. Broadly speaking the sediments can be regarded as being a broad area of muddy sand divided down the middle by a strip of sandy silt which corresponds to a tongue of deep water (80–100 m) running approximately north to south at a distance of about 15 miles offshore all along the southern half of the Northumberland coast. The inshore strip of muddy sand is itself divided approximately down the middle by a long tongue of almost clean sand over 20 miles in length and varying from 1 to 7 miles in width at depths of 40–60 m. The offshore area of muddy sand also has areas, like the inshore, which as a result of tidal scour are swept almost clean of fine sedimentary material. It is on these sandy areas both inshore and offshore that *A. limicola* is a constant and conspicuous constituent of the benthic fauna. The bottom in these areas is fine to medium sand (250–500 μ) with generally less than 10% silt (particles less than 62 μ) and less than 2% clay (particles less than 4 μ). It should be emphasized that these sandy areas are isolated patches or strips surrounded by muddy sand and that their fauna does not represent a discrete community of species, but rather a modification of the fauna found on the muddy sand surrounding them, which can be broadly described as belonging to the classical 'Echinocardium-filiformis' community of Petersen.

Fifty-six stations were sampled with a Van Veen grab throughout the extent of the sandy area with *A. limicola* occurring in 82% of the hauls at an average density of 53 specimens per square metre, the greatest density being 240 individuals per square metre. The animals found commonly in this association are listed in Table 1.

TABLE 1. OTHER ANIMALS FOUND ASSOCIATED WITH *A. LIMICOLA* WITH THEIR AVERAGE NUMBERS PER SQUARE METRE FOR FIFTY-SIX HAULS

	No. per m^2
Astrorhiza limicola	53
Amphiura filiformis	47
Nephthys spp.	13
Owenia fusiformis	5
Echinocardium flavescens	4
E. cordatum	1
Goniada maculata	4
Dosinia lupinus	4
Dentalium entalis	4
Echinocyamus pusillus	4
Venus striatula	3
Ampelisca brevicornis	2
A. macrocephala	1
Phaxas pellucidus	2
Sthenelais limicola	2
Astropecten irregularis	2
Abra prismatica	1

Quantitative data are sparse for other areas but two records are worth noting. Stephen (1923) reports the rhizopod from a grab haul taken at a depth of 101 m off the Butt of Lewis where ten specimens were obtained in 0·1 m^2, together with *Echinocardium flavescens*, *Dentalium entalis*, *Ophiura affinis*, *Abra prismatica* and *Mactra elliptica*. Secondly, an association similar to that found off Northumberland has been described by Caspers (1950) from off the Heligoland coast. Here *Astrorhiza limicola* reached a maximum density, in one haul, of sixty-seven individuals in 0·1 m^2 but this high density appears to be confined to a very small area. Figures given by Caspers (1950) for the particle size analysis of the bottom sediment also appear to be very similar to the Northumberland sediments and consist mainly of sand fractions from 125 to 500 μ at a depth of 22–25 m. The associated animals off Heligoland are *Amphiura filiformis*, *Owenia fusiformis*, *Nephthys* spp., *Venus striatula*, *Spisula solida*, *Cochlodesma praetenue*, *Echinocyamus pusillus* and *Phoronis mulleri*. In both the Northumberland and Heligoland areas the ecological conditions appear to be very similar and both are isolated sandy areas more or less surrounded by a typical 'Amphiura' community. Thorson (1957) suggested that the Heligoland association, in which *Astrorhiza limicola* is dominant, may be regarded as a 'Foraminifera' community, whereas we are of the opinion that this association should be regarded as a variation or faciation of the 'Amphiura' community (Thorson, 1957) where it is in a state of transition to a 'Venus' community. This transition is never completed off the Northumberland coast, since the sediments rapidly become more muddy again as deeper water is approached and the characteristic associations of a true 'Venus' community are never found to be sufficiently significant to dominate the population.

Dense populations of *A. limicola* always appear to be associated with stable areas of fine to medium sand, with only small amounts of silt and clay, containing a relatively rich interstitial fauna. Such areas seem to lie intermediate, in bottom conditions, between the muddy sand areas, with slow bottom currents allowing quantities of silt and clay to accumulate, and clean sand areas with relatively strong bottom currents and probably less interstitial stability. In the few areas which have been quantitatively studied the intermediate bottom conditions are confirmed by a fauna, occurring with *A. limicola*, which is generally in the nature of a mixed community.

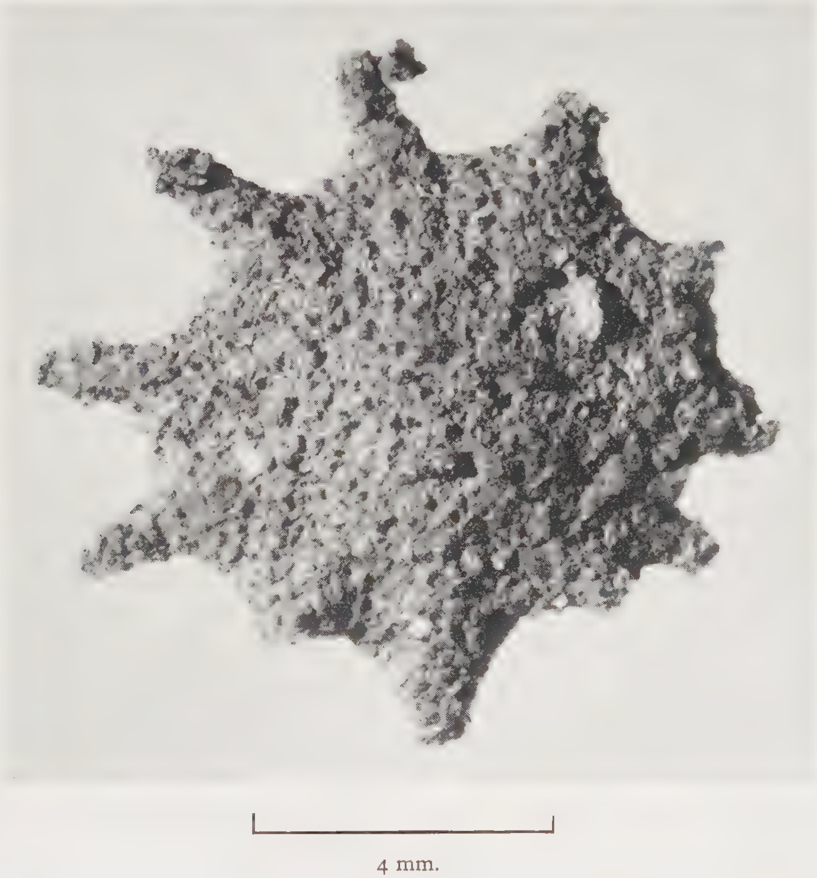

Fig. 1. A typical *Astrorhiza limicola* collected from the Northumberland coast.

STRUCTURE OF THE TEST

Individuals of *A. limicola* are surrounded by a well-defined stellate test built up of extraneous material from the bottom sediments on which they lie (Figs. 1, 2). In addition to this foreign material there is an organic cement, secreted by the animal, causing the sand grains to cohere and ensuring the stability and form of the arenaceous test.

The extraneous constituents

In the Northumberland specimens the tests are constructed for the most part from inorganic material in which quartz grains predominate, although other materials, such as shell fragments and small echinoderm spines, are often incorporated. Although quantitative sampling has shown that the rhizopods occur in the largest numbers on the clean, comparatively silt free, sands, they can be collected in small numbers over a wide range of bottom conditions from fine silty sand to clean coarse sand. Individuals collected from these different areas show obvious superficial differences in external appearance suggesting that the material utilized in test building is obtained in a non-selective manner. Furthermore, in laboratory experiments *A. limicola* will readily utilize such materials as powdered glass and 'Perspex' shavings to effect a repair of a damaged test.

A large sample of individuals collected from several different types of sea bottom was treated with sodium hypochlorite solution resulting in the destruction of the organic matter and leaving a dispersed sample of the inorganic constituents of the test. Particle size analysis of this material showed that a complete range of particles was present from somewhat over 1000 μ down to slightly under 30 μ. Several other samples of *Astrorhiza* were similarly analysed along with analyses of the bottom sediment from which they were collected. It was found that for any particular locality the material in the test and the material from the bottom sediment produced an almost exact correspondence in analysis figures, indicating, that with the exception of the coarsest material and fine gravels, the animal incorporates the bottom sediment material into its test in almost exactly the same proportions as it is found in the sediment samples.

Specimens obtained from Plymouth had tests constructed of rather coarse sand and shell particles indicating that the bottom on which they lie is probably of shelly-gravel and coarse sand. The superficial difference between these specimens and those from the muddier areas of Northumberland is very marked, again suggesting that the nature of the material incorporated into the test appears to have little significance.

The organic cement

Microscopic examination and manipulation of a portion of the test wall shows this interstitial substance to have the consistency of a rigid gel, whereas after fixation in alcohol and in dried specimens, it is very contracted, giving the impression that little organic cement is present.

The cement has an affinity for basic dyes; it stains when immersed in a 0·01 % aqueous solution of toluidine blue, exhibiting γ-metachromasia when examined in water (Pearse, 1953) and reacts positively with Schiff's reagent after prior oxidation with periodic acid (Hotchkiss, 1948). Attempts to demonstrate the presence of certain amino acids, and thereby protein, by the Millon and Sakaguchi reactions, have not been successful, although a positive result was obtained after the coupled tetrazonium reaction procedure for tyrosine, tryptophane or histidine (Pearse, 1953). From these results it appears that the cement is a protein-carbohydrate material with part at least being an acid mucopolysaccharide. Little more of any significance can be said about the chemical composition of the cement in the absence of a full analysis. It can, however, be referred to as 'tectin' (Hyman, 1940), although it must be emphasized that this term implies no precise chemical composition beyond the fact that the substance is composed of protein and carbohydrate in combination, that is, a type of glycoprotein. As there are many different forms of glycoproteins so there will be many different tectins.

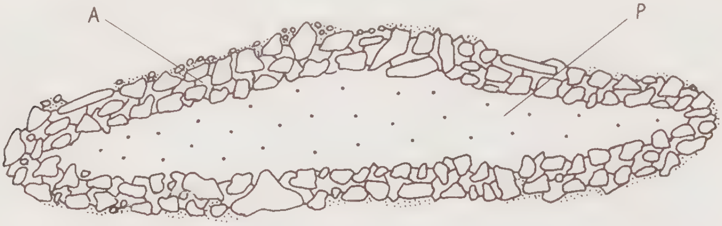

Fig. 2. A diagrammatic transverse section of *Astrorhiza limicola*. *A*, arenaceous wall; *P*, protoplasm.

The 'inner chitinous lining' of the test

The term 'chitinous' has often been used in foraminiferal work as an adjective of convenience to describe any of a variety of organic structures, including a thin lining to the interior of the test wall in *A. limicola* (Cushman, 1948). No worker, to the authors' knowledge, has demonstrated chitin in any part of the test of *A. limicola*, or indeed in any arenaceous foraminifer, and as no organic residue has been found after boiling in caustic potash there is no reason to suppose that chitin is present.

The inner organic layer of the test, just referred to, has some taxonomic significance, for Stschedrina (1946) notes that *A. limicola* var. *arenifera* differs from the typical *A. limicola* in having a more fragile and thin test and in the absence of an 'inner chitinous lining'. It must be pointed out that to the authors' knowledge the inner lining to the test of *A. limicola* has never been described or figured, and the question arises, does one exist at all? The following observations are relevant to this problem.

None of the living specimens from Blyth and Plymouth which have been examined possessed a recognizable inner organic lining to the test, nor was there an excessively large amount of organic cement on the internal surface which could have been mistaken for a distinct inner layer. In alcohol-preserved and particularly dried specimens, however, the protoplasm has invariably changed colour from the normal cream to a dark red-brown and with the resultant dehydration the shrivelled protoplasm has assumed positions, especially in the radiating arms, which give the impression of a brown organic lining. It is quite likely that this abnormal state may account for some of the categorical statements of the presence of an inner lining, especially when it is noted that many faunistic accounts of Foraminifera have been based on dry collections.

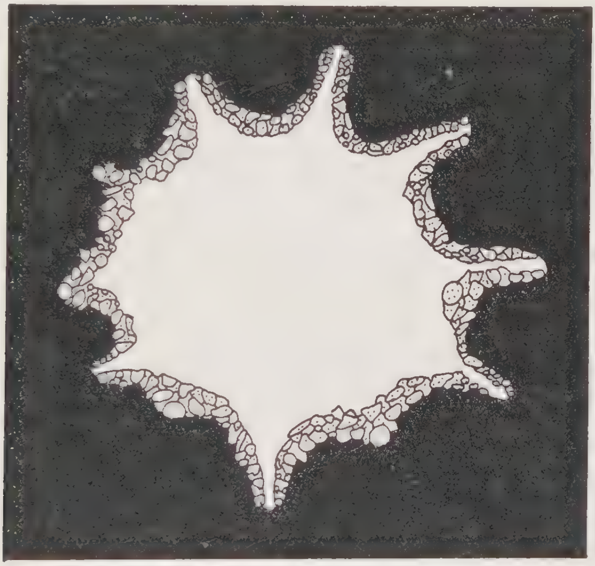

Fig. 3. A diagrammatic top view of *Astrorhiza limicola* after the roof has been removed to reveal the internal creamy protoplasm.

Another way in which the 'inner lining' character may have become established in the literature is through the examination of specimens which have at some time been damaged and have subsequently undergone repair. Although no examples of this sort have been collected by us, certain laboratory experiments of a damage and repair nature have been carried out, and the results may have some bearing on the problem. If, for example, the roof of a test is removed leaving the creamy protoplasm exposed (Fig. 3) and this damaged animal is left in a container without sand grains it will always secrete a membrane (Fig. 4), usually within 12 h. This organic membrane is approximately 10 μ thick, separate from and independent of the protoplasm which has secreted it, and completely covers that part of the test which has been damaged. If a damaged animal such as this is now placed in a container with sand grains these are manoeuvred by the pseudopodia on to the membrane and cemented to it until the wall appears normal. In this case *A. limicola* does have an inner organic lining to the test, but only to that part which has been repaired. When animals are placed among sand grains immediately after being damaged they usually repair their tests by incorporating the sand grains on the exposed surface without the secretion of a definite foundation membrane. There is, however, no precise procedure which can be said to take place in every case. If the animal is squeezed out of the test and left naked in a container free of sand grains it soon secretes a membranous test, completely surrounding the protoplasm.

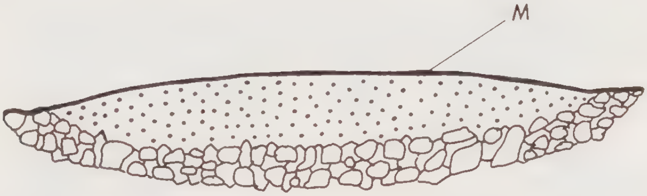

Fig. 4. A diagrammatic transverse section of *Astrorhiza limicola* to show the position of an organic membrane, *M*, mentioned in the text.

These membranes react with stains similarly to the cement of the test wall. They are isotropic, have the appearance of a relatively strong proteinaceous structure, and, in almost all instances, are clear and transparent when newly formed, becoming brown and translucent after a few days.

It is concluded that normally *A. limicola* does not possess a distinct lining of organic material on the interior wall of the test, although under certain rather unusual conditions an organic membrane is secreted.

The presence of iron in the test

The ferruginous nature of *A. limicola* is demonstrated when the sand grains and organic cement are coloured blue after immersion in acidified potassium ferrocyanide (equal parts 2% hydrochloric acid and 2% potassium ferrocyanide). This production of the Prussian blue compound is the end product of a specific reaction and chemical test for ferric iron. The presence of iron in the tests of a number of other arenaceous forms has been commented upon by Vinogradov (1953) and a question of some interest is whether the source of the iron is directly from the immediate environment or whether it is being secreted by the animal. The same problem is discussed by Hedley (1960) in relation to *Gromia oviformis*, a rhizopod with an organic test, where it does appear that the animal is secreting iron in some form which, in part at least, is deposited in the test wall. As far as the arenaceous foraminifera are concerned Vinogradov (1953) summarizes the available data and infers that there is an active physiological process whereby iron is 'precipitated' by the animals. One of us is currently investigating a number of arenaceous forms with this problem in mind, so that at this stage only those observations on *A. limicola* will be discussed: (*a*) Tests for iron in the protoplasm, using 6 μ paraffin sections, have failed to reveal any structures which are iron positive. (*b*) Freshly secreted membranes of damaged animals are iron negative. (*c*) If *A. limicola* is placed in a dish containing sand grains from the sediment in which it was living at the time of collection, but which have been treated with concentrated hydrochloric acid to remove the iron and then thoroughly washed, any subsequent addition to the test, either sand grains or organic cement, is iron negative.

The foregoing observations suggest that the ferruginous nature of the test wall is the result of the iron already present on the sand grains of the sediment which are incorporated into the test by the animal. Consequently at this stage there is no evidence of the animal secreting iron.

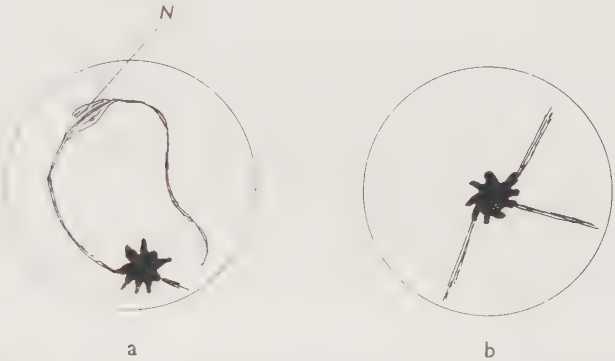

Fig. 5. Drawings showing the extent of two pseudopodial systems as they were seen when individuals were isolated in plastic dishes in the laboratory. The black circles represent the edges of the dishes and the nodule, N, is noted in the text (natural size).

BEHAVIOUR

The presence of epizoic growths of hydroids, ascidians and other arenaceous foraminifera on the upper surface of many tests of *Astrorhiza* shows that the animal normally lives on the sand surface and does not burrow. This was confirmed by observation of living material in the laboratory. When freshly collected animals are isolated in dishes with a sand substratum, they move in a more or less elliptical path for considerable distances. Schultz (1915) noted a distance of 25 cm covered in 24 h and speeds of this order have been confirmed on several occasions. The distance and route covered by isolated animals can be easily observed, since a furrow is left in the sand as a result of the leading edge of the test being preceded by a raised mound or 'bow-wave' of sand. When movement ceases this mound of sand may cause the test to appear buried to a very small extent. After a period of roaming about the dish, often lasting 24 hr, the animal settles and proceeds to develop an extensive pseudopodial system.

The pseudopodia ramify both over the sand surface and through the interstitial spaces to a depth of about 2–3 mm below the surface. Naturally they are more readily observed in dishes without a sand substratum and in such cases it is apparent that the pseudopodia occasionally have relatively large masses of protoplasm, forming nodules, along their length. Two typical pseudopodial arrangements are presented in Fig. 5a, b. Bessels (1875) drew a group of *Astrorhiza* showing seven specimens connected together to form a network, but we have not observed any actual union of different pseudopodial systems or of tests belonging to two or more individuals. Nevertheless a sediment inhabited by a number of *A. limicola* must be regarded as being very extensively ramified by their pseudopodia which may extend to distances of more than 6–7 cm from the central protoplasmic mass of each individual.

Feeding

At an early stage during the observations it became clear that the pseudopodia can exist in what will be referred to here as two physiological states. In the first of these the pseudopodia are very adhesive, so that, when the pseudopodial system ramifies through a sandy substratum, any particle sticks to it immediately and is held tenaciously. At other times, with the pseudopodia apparently in another physiological state, there is no adhesive property at all. In order to test the possible capabilities of the pseudopodia for catching live animals such as would normally be present in the natural habitat, several individuals were isolated in dishes and given time to develop a pseudopodial system. A variety of live animals ranging from small copepods and amphipods to nematodes and small echinoderms were then introduced. Although these animals were in a healthy state and moving briskly, they were firmly held whenever they came in contact with the adhesive pseudopodia. *A. limicola* proved itself quite capable of holding and eventually immobilizing such animals as fully grown cumaceans (*Diastylis laevis*), caprellids up to 2–3 cm in length and small recently metamorphosed *Echinocardium flavescens* as well as a variety of small crustacea. Similar experiments were carried out in dishes with a sandy substratum into which actively swimming *Artemia* were introduced. Whenever an *Artemia* landed on the bottom at a point where the pseudopodia were exposed it was firmly held. In all these experiments the captured animals struggled for long periods, invariably in vain, gradually becoming weaker and eventually dying. On examination after a period of 1–2 days nothing remained of a caught animal other than a clean cuticle.

There is no evidence that a toxin is secreted by *Astrorhiza* to kill the animals after they have been caught by the pseudopodia. Observations of the process tend rather to support the opinion that the prey gradually dies through exhaustion and perhaps suffocation as a result of being firmly held by the pseudopodia. As no process of ingestion has been observed it is implicit that there is some process of extracellular digestion such as is said to occur in the case of *Elphidium crispum* (Jepps, 1942).

From the information obtained from laboratory feeding experiments there would seem to be strong evidence that *Astrorhiza limicola* is an active, mobile predator of the interstitial sand fauna and of the smaller faunal elements associated with the sediment surface. Schultz (1915) suggested that it feeds on small protozoans and flagellates, and from sections we have seen that diatoms are ingested. It seems likely that just as the animal is non-selective in test building it is also not very selective in feeding. If, as seems probable, interstitial organisms constitute the main food supply, the interstitial microfauna of those areas where *A. limicola* occur in large numbers must be profoundly affected.

SUMMARY

A general account, based on literature records, is given of the distribution of *Astrorhiza limicola* in addition to a more detailed account of its distribution and ecology off the Northumberland coast. The animal is seen to be non-selective of the materials used for test construction and an account of the test structure considers the significance of its ferruginous nature, the organic cement component secreted by the animal, and an 'inner chitinous lining' often reported in the literature.

Laboratory observations of living animals indicate that *A. limicola* may be regarded as a mobile predator of interstitial sand metazoans.

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AMPHIBDELLID (MONOGENEAN) PARASITES OF ELECTRIC RAYS (TORPEDINIDAE)

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(Plates I–III and Text-figs. 1–28)

Electric rays (Torpedinidae) are known to harbour on their gills certain monogenean parasites (*Amphibdella* spp. and *Amphibdelloides* spp.) whose taxonomy is in a very confused state. Much of this confusion has centred around a single morphological feature: a 'transverse bar' has been variously held to be present or absent from the adhesive apparatus, or sometimes two such bars have been stated to be present. Among those who have regarded the transverse bar as having taxonomic importance, Price (1937) recognized two genera of amphibdellids distinguishable by the presence or absence of the bar, but Palombi (1949) and Bychowsky (1957) believe that the bar may be present in young specimens but absent or inconspicuous in older specimens. No-one has investigated the function of this transverse bar, or, indeed, any functional aspect of the adhesive apparatus. Again little attention has been paid in taxonomy to the genitalia or host specificity, or, in spite of a record of an amphibdellid from the heart of its host, to micro-habitat.

As part of an attempt to repair these omissions, a general watch was kept for electric rays landed by the research vessels at Plymouth in July and August in the period 1953–59. During this time only three specimens of *Torpedo nobiliana* were brought in, but fortunately these yielded supplies of the parasites in question. In addition, as a result of the most helpful cooperation on the part of the Staff of the Plymouth Laboratory, especially Mr J. E. Green, fresh gills of a further two specimens of *T. nobiliana* were sent to Birmingham in October 1956 and September 1959, respectively, and were found to bear living parasites.

Amphibdellids were collected from three distinct micro-habitats on *T. nobiliana*, and for reasons to be given later (pp. 580–5) were identified as follows:

1. Secondary gill lamellae (see Pl. I, fig. 2)	*Amphibdelloides maccallumi* (Johnston & Tiegs, 1922) Price, 1937
2. Parietal mucosa of gills (see Pl. I, fig. 1)	*Amphibdella flavolineata* MacCallum, 1916. Adult specimens
3. Cavity of heart	*A. flavolineata* MacCallum, 1916. Juvenile specimens

Amphibdelloides maccallumi was found to be very common, some 100 to over 2000 specimens being present on each of the five host specimens examined; adult specimens of *Amphibdella flavolineata* were found on the gill mucosa of four of the five host specimens, the maximum infestation being six parasites per host; and juvenile specimens of *A. flavolineata* were found in the heart of two host specimens, one of these hosts bearing two parasites, and the other a single parasite.

All these parasites were studied living and *in situ*, as living specimens under pressure of a cover-glass, as stained whole mounts, and by means of paraffin sections. In studying the adhesive apparatus, whole specimens relaxed in propylene phenoxetol (Owen, 1955), mounted freely in glycerol, and examined stereoscopically, were especially useful, as also was phase-contrast microscopy of flattened whole mounts in balsam.

These monogenean parasites of *Torpedo nobiliana* at Plymouth have been compared with various amphibdellid parasites from electric rays from other regions as indicated in Table 1, in which the hosts have been named as in Bigelow & Schroeder (1953). As a result of the comparison it became necessary to propose certain taxonomic revisions. For convenience these are listed in Table 1 but the taxonomic diagnoses will be given later (pp. 580–2) following descriptions of the kinds of characters used in the recognition of the different species.

MICRO-HABITAT

Amphibdelloides maccallumi lies between two adjacent secondary gill lamellae (Pl. I, fig. 2) with its posterior end in contact with the primary lamella (Pl. II, fig. 1). It maintains this position by the use of two pairs of hooks, one pair directed dorsally and the other ventrally. These hooks are inserted into the bases of the secondary lamellae, the points of the hooks often emerging on the other side of the lamella.

Adult specimens of *Amphibdella flavolineata* attach themselves to the proximal region of a primary gill lamella, i.e. a region adjacent to the interbranchial septum and lacking secondary lamellae (Pl. I, fig. 1), and referred to in *Torpedo torpedo* by Parona & Perugia (1890, p. 364) as 'mucosa parietale'. The whole of the relatively bulky haptor is accommodated subcutaneously within the host tissues, the remainder of the body of the parasite being connected to the haptor by a neck region which is constricted by the superficial tissues of the host (Pl. II, fig. 2).

Amphibdelloides vallei attaches itself to the gills of *Torpedo marmorata* (Pl. I, fig. 3) in exactly the same manner as does its counterpart *Amphibdelloides maccallumi* to *Torpedo nobiliana*, but there is less correspondence between the attachment of *Amphibdella torpedinis* to *Torpedo marmorata* and that of *Amphibdella flavolineata* to *Torpedo nobiliana*. Although *Amphibdella torpedinis* attaches itself to the parietal mucosa rather than to the secondary

TABLE 1. TAXONOMIC DESIGNATIONS, HOSTS, AND GEOGRAPHICAL SOURCES OF AMPHIBDELLID SPECIMENS STUDIED

Host	Locality	Author/ collector	Parasites	
			Genus *Amphibdelloides* Price, 1937	Genus *Amphibdella* Chatin, 1874
Torpedo nobiliana Bonaparte syn. *Tetronarce occidentalis* Storer syn. *Tetranarce occidentalis* Storer	Irish Sea Irish Atlantic Slope Sète, Mediterranean Wood's Hole, U.S.A. Plymouth	Rees & Llewellyn (1941) Dr H. H. Williams Dr L. Euzet MacCallum (1916) Llewellyn	*Amphibdelloides maccallumi* (Johnston & Tiegs, 1922) Price, 1937 syn. *Amphibdella maccallumi* Johnston & Tiegs, 1922 syn. '*Amphibdella torpedinis* Chatin' of MacCallum (1916)	*Amphibdella flavolineata* MacCallum, 1916
Torpedo californica Ayres	California	Alexander (1954)	*Amphibdelloides maccallumi* (Johnston & Tiegs, 1922)	—
Torpedo marmorata Risso	Sète, Mediterranean	Dr L. Euzet	*Amphibdelloides vallei* sp.nov. syn. '*Amphibdelloides maccallumi*' of Euzet (1957) in part syn. '*Amphibdella torpedinis*' of Perugia & Parona (1889) = Valle's specimens from Trieste	*Amphibdella torpedinis* Chatin, 1874
Torpedo torpedo (L.) syn. *T. narke* Risso syn. *T. ocellata* Rudolphi syn. *Raja narce* Nardo	Genoa, Mediterranean	Parona & Perugia (1890)	—	*Amphibdella paronaperugiae* sp.nov. syn. '*Amphibdella torpedinis* Chatin' of Parona & Perugia (1890) and Ruszkowski (1931)
Narcine brasiliensis (Olfers)	Florida	Hargis (1955)	*Amphibdelloides narcine* Hargis, 1955	

lamellae, it may be found not only on the proximal region of the primary lamella (Pl. I, fig. 4B), i.e. near to the interbranchial septum, as in *A. flavolineata*, but on the distal region as well (Pl. I, fig. 4A); like *A. flavolineata*, *A. torpedinis* buries the posterior end of its body subcutaneously in its host.

I have not seen attached specimens of *Amphibdelloides narcine* or *Amphibdella paronaperugiae*, but Parona & Perugia (1890, p. 364) stated that the latter species was attached to the 'mucosa parietale'.

The three juvenile specimens of *A. flavolineata* collected in the present study were all found among the loosely woven muscle strands in the ventricle of the heart, and did not appear to be attached to the host tissue. Other parts of the blood system of *Torpedo nobiliana* were not searched. Juvenile specimens of *Amphibdella torpedinis* were collected for me from the heart of *Torpedo marmorata* by Dr Louis Euzet.

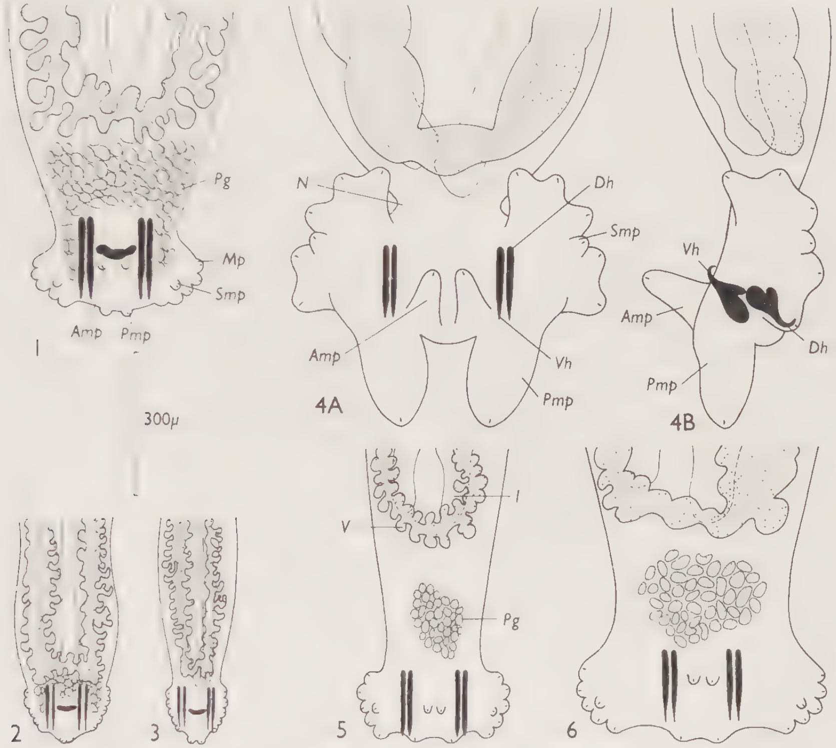
The micro-habitat of juvenile specimens of *Amphibdella flavolineata* and *A. torpedinis* thus differs from that of any other known monogenean, excepting Ruszkowski's (1931) specimens of *A. paronaperugiae* (syn. *A. torpedinis*) from the blood system of *Torpedo torpedo*. By far the greater number of monogeneans are ectoparasitic, but a few are endoparasitic in the coelom, oviducts, ureters, or urinary bladders of their hosts (see Llewellyn, 1957). The invasion of the blood system of an elasmobranch by a monogenean is not likely to have incurred undue physiological problems: food and oxygen supplies would change but little, and the osmotic relations with the ambient medium would also be relatively unchanged, since elasmobranchs are known to be approximately isosmotic with sea water (Smith, 1936). Probably the greatest novelty was the assumption of a tolerance of the high urea concentrations known to be present in elasmobranchs (Smith, 1936). The egg capsules could be released when the anterior end of the parasite emerges through the gill tissues to take up the definitive adhesive attitude illustrated for *Amphibdella flavolineata* in Pl. II, fig. 2.

ATTACHMENT TO THE HOST

The haptor of amphibdellids may contain three kinds of adhesive apparatus: 'hooklets' (= persistent oncomiracidial hooks) borne on papillae; large hooks, with or without an accessory sclerite (= 'transverse bar'); and glands.

Hooklet-bearing papillae

Along the lateral margins of the haptor of *Amphibdelloides maccallumi* are borne, on each side, six very labile muscular papillae (Text-fig. 1); five of these are truly marginal, but the remaining one is submarginal on the ventral surface immediately medial to the interval between the 3rd and 4th marginal papillae from the anterior end. In addition to these six pairs of papillae, two other pairs are present: first, a median pair on the posterior margin of the haptor, separated by a relatively wide interval from the remaining marginal (lateral) papillae, and secondly, a median pair on the ventral surface of the body immediately posterior to the transverse bar of the main hook-apparatus (see below). Each of the sixteen papillae bears an apical hooklet of about 6–8 μ long. These papillae are often obliterated if the usual practice is followed of flattening specimens before mounting them; the papillae are best seen in living specimens or in specimens relaxed in propylene phenexetol.



Text-figs. 1–6. The haptors of amphibdellids, all drawn to the same scale. Fig. 1. *Amphibdelloides maccallumi*. Fig. 2. *A. vallei*. Fig. 3. *A. narcine*. Figs. 4A, B. *Amphibdella flavolineata*, 4A ventral view, 4B side view. Fig. 5. *A. paronaperugiae*. Fig. 6. *A. torpedinis*. *Amp*, anterior median papilla; *Dh*, dorsal hook; *I*, intestine; *Mp*, marginal papilla; *N*, neck; *Pg*, posterior gland; *Pmp*, posterior median papilla; *Smp*, submarginal papilla; *V*, vitellarium; *Vh*, ventral hook.

In *A. vallei* (Text-fig. 2) and *A. narcine* (Text-fig. 3) the haptor is less expanded laterally than in *A. maccallumi*, and in dorsal or ventral view is approximately triangular with the apex directed posteriorly. Suitably treated material for a detailed study of the distribution of the papillae in these two species was not available.

In *Amphibdella flavolineata* (Text-figs. 4A, B) there is a very well-marked neck region separating the haptor from the body-proper, the narrowness of the neck being emphasized by the great expansion of the haptor in the subcutaneous tissues of the host (Pl. II, fig. 2). The two median pairs of papillae are very much larger than the lateral marginal ones: the posterior median papillae are greatly extended in a posterior direction (Text-fig. 4A) and the anterior median papillae are greatly extended in a ventral direction (Text-fig. 4B). The lateral papillae are borne on a considerably expanded flange that is obliquely disposed with respect to a horizontal plane of the haptor (Text-fig. 4B). This spreading of all of the hooklet-bearing papillae of *A. flavolineata* in several planes has the effect of securing more effective 'rooting' in the deep-seated tissues of the host.

In *A. paronaperugiae* (Text-fig. 5) and *A. torpedinis* (Text-fig. 6) the shape of the haptor is very similar to that of *Amphibdelloides maccallumi*, i.e. the hook-bearing papillae do not become expanded as they do in adult specimens of *Amphibdella flavolineata.*

In *juvenile* specimens of *A. flavolineata* the haptor resembles that of *adult* specimens of *A. torpedinis* and *A. paronaperugiae* (and thus also that of *Amphibdelloides maccallumi*), i.e. the hooklet-bearing papillae have not yet become expanded.

In all six amphibdellid species studied, the correspondence is obvious between the hooklet-bearing papillae of the adult and the hooks of the oncomiracidium described by Euzet (1957) as '*A. maccallumi*'.

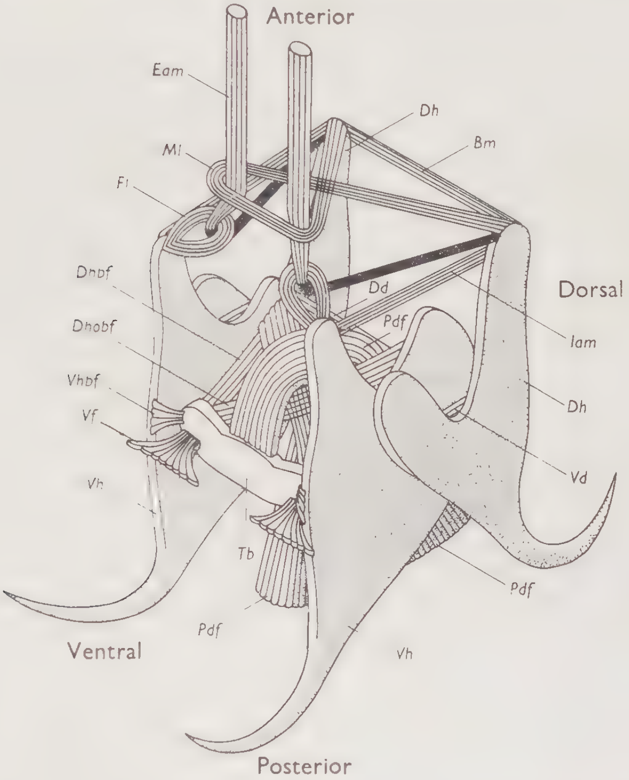
Large hooks

The principal adhesive apparatus of *A. maccallumi* (Text-fig. 7 and Pl. III, figs. 1–6) consists of two pairs of hooks, a median (= inner) pair with the points directed ventrally (*Vh*) and a flanking (= outer) pair with the points directed dorsally (*Dh*). These hooks are supported by a transverse bar (*Tb*) and are operated by a complex system of muscles.

The transverse bar is a flattened structure of the shape illustrated in Text-figs. 7 and 8C, i.e. it consists of a median region and two antero-laterally inclined lateral regions. This bar lies transversely in the ventral region of the body at a position approximately midway along the length of the hooks. It is suspended from the integument of the body by two antagonistic systems of fibres: one set (*Vf*) joins the lateral regions of the bar directly to the integument of the ventral surface of the body, and the other, more powerful set (*Pdf*) curves dorsally and then posteriorly from the anterior surface of the transverse bar to the integument of the dorsal and posterior regions of the haptor.

It is not known whether these fibres are contractile, but their function appears to be that of anchoring the transverse bar firmly to the integument. It will be shown later than when the main hook-operating muscles contract there would be a tendency for the hooks to be drawn forwards in the body were they not attached to a bar which is itself tethered to resist a pull in this direction.

The hooks are of the form illustrated in Text-figs. 8 A and B. There is a slight but characteristic dissimilarity between the ventral and dorsal hooks, the former being the larger, especially in the 'shoulder' region. The distal curved regions of all four hooks are strongly birefringent, but the proximal blade-like regions much less so. All parts of the hooks may be differentially stained with malachite green, and, less readily so, with haematoxylin. Such is the affinity of the strongly birefringent regions for picric acid that, following fixation in Bouin's fluid, they remain yellow even after prolonged immersion in alcohol, and subsequent staining with haematoxylin is inhibited. At the place where the tip of each hook leaves the body it is surrounded by a muscular sheath (Pl. III, fig. 1, *Ms*) which, in living specimens forcibly detached from the host, has been seen to oscillate rhythmically along the length of the basal region of the curved portion.



Text-fig. 7. The principal adhesive apparatus of *Amphibdelloides maccallumi*. For explanation of lettering see text pp. 566–9.

Each ventral hook is attached to the transverse bar by three bundles of fibres: short fibres from the ventral edge of the hook to the adjacent lateral ends of the transverse bar (*Vhbf*); long fibres from the dorsal region of the inner (= medial) surface of the hook to the lateral end of the transverse bar on the same side of the parasite (*Dhbf*); and long fibres from the same region of the hook (i.e. the dorsal region of the inner surface) obliquely ventrolaterally to the dorsal surface of the lateral region of the transverse bar on the other side of the parasite (*Dhobf*).

Each dorsal hook is attached to the ventral hook of the same side of the animal by fibres which pass from the ventral edge of the inner surface of the dorsal hook to the dorsal edge of the outer surface of the ventral hook (*Vd*). Some of these fibres, lying posterior to the level of the transverse bar, are not attached to the dorsal edge of the ventral hooks; instead they pass transversely across the body, dorsal to the dorsal edges of the ventral hooks, and become continuous with their fellows of the opposite side (*Dd*). Those fibres inter-connecting the ventral and dorsal hooks (*Vd*) serve to bind these hooks to each other in a manner that permits the rotation of these hooks, in the planes of their flat surfaces, about their regions of mutual attachment. The fibres connecting the two dorsal hooks with each other (*Dd*) probably serve to brace the whole system of hooks and fibres.

While the fibrous systems connecting the ventral and dorsal hooks (*Vd*) *could*, if they were indeed contractile, rotate the posterior parts of the hooks in opposite directions about the region of the transverse bar, nevertheless, the main actuation is produced by the contraction of a system of muscles attached to the anterior ends of the hooks. The proximal (anterior) end of each ventral hook bears a fibrous loop (*Fl*) through which passes the main extrinsic adductor muscle (*Eam*) of the same side of the body on its way to become attached to the proximal (anterior) end of the dorsal hook (*Dh*) of the same side. The part of the muscle passing through the loop, and its continuation to the dorsal hook are considerably narrower in diameter than the remainder of the muscle. In appearance this region resembles the tendons of the adhesive apparatus of *Plectanocotyle gurnardi* and *Kuhnia scombri*, but, unlike such tendons, they take up haematoxylin and xylidine ponceau and not light green in Masson's trichrome stain.

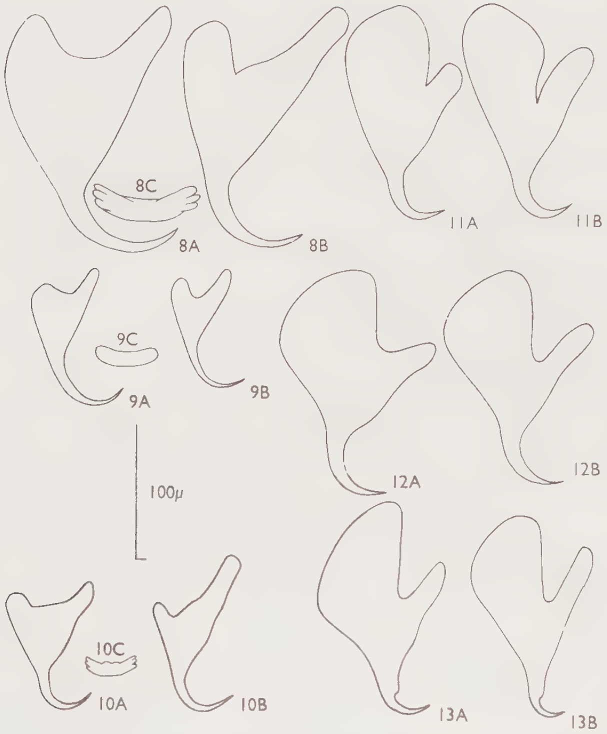
Since the hooks are pivoted about the transverse bar, contraction of the extrinsic adductor muscles (*Eam*) would draw the proximal ends of the dorsal and ventral hooks towards each other, and so cause the distal tips of the ventral hooks to rotate ventrally, and the distal tips of the dorsal hooks to rotate dorsally. When the parasite is located between successive secondary gill lamellae, such movements would result in the hooks impaling these lamellae and so securing the parasite to its host (Pl. II, fig. 1).

The action of the main extrinsic adductor muscles is augmented by the contraction of smaller intrinsic adductor muscles (*Iam*) connecting directly with one another the proximal ends of the dorsal and ventral hooks on the same side of the body. The proximal ends of the dorsal hooks are connected to each other by a bracing muscle (*Bm*).

From the proximal end of each of the dorsal hooks a muscle passes ventrolaterally towards the other side of the body, crosses its fellow from the other side, and then contributes to the formation of a single median loop (*Ml*) that surrounds the two extrinsic adductor muscles at a position immediately anterior to where these muscles become narrower before being threaded through the fibrous loops on the proximal ends of the ventral hooks. The function of this median loop is not obvious, but two possibilities are suggested: first, it could serve as a brace for the ventral components of the extrinsic adductor system; secondly, a tonic contraction of this loop about the narrow parts of the extrinsic adductor muscles would simulate a 'catch' mechanism and so relieve these muscles of the burden of continuous contraction; the relaxation of these adductor muscles (which stretch anteriorly more than half way along the animal) would permit exploratory movements of the body proper to be made more freely.

The hooks (and transverse bar when present) in the different species of amphibdellids exhibit characteristic variations in shape and size as indicated in Text-figs. 8–13. It is to be noted that in *Amphibdella paronaperugiae* (Text-figs. 13A, B) there is a distinct shoulder at the junction of the flattened blade with the slender curved part of the hook. This shoulder was found to be present in all four hooks of each of ten specimens from *Torpedo torpedo* examined, as, indeed, had been illustrated previously by Ruszkowski (1931) in amphibdellid parasites from the same host species. In a similar sample of ten specimens of *Amphibdella torpedinis* from *Torpedo marmorata* no corresponding shoulder was found, but Chatin (1874) had illustrated a shoulder region in the hooks of his *Amphibdella torpedinis* specimens which were said to have been collected from the same host species. The absence of a shoulder region in the hooks was used by Price (1937) as the principal distinction between *A. flavolineata* MacCallum, 1916 and Chatin's *A. torpedinis*. The evidence from the present study of amphibdellids suggests very strongly that either Chatin's drawing of the hooks, or his identification of the host, was inaccurate. Since the remainder of Chatin's description of *A. torpedinis* would be grossly inaccurate for any amphibdellid, it is proposed here to disregard his description of the shape of the hook, and to accept his identification of the host.

The muscles associated with the hooks and transverse bar in *Amphibdelloides vallei* and *A. narcine* are arranged exactly as those in *A. maccallumi* described above. In *Amphibdella flavolineata*, *A. torpedinis*, and *A. paronaperugiae* there is no transverse bar, and the fibres associated with such a bar in *Amphibdelloides* are absent. In *Amphibdella torpedinis* and *A. paronaperugiae* the adductor muscle system differs from that of *Amphibdelloides* *maccallumi* in that no median loop (*Ml* in Text-fig. 7) is present, but the 'bracing muscle' (*Bm* in Text-fig. 7) is relatively much better developed. The hook muscles in *Amphibdella flavolineata* are arranged completely differently from those of the other five amphibdellid species studied: there are no fibrous loops on the proximal ends of the ventral hooks (*Fl* in Text-fig. 7), there is no 'median loop' (*Ml* in Text-fig. 7) and there are no muscles connecting the hooks of the left side of the parasite with those of the right. The muscles that are present consist of simple longitudinally running bundles, one relatively weak bundle from each hook going posteriorly to the integument between the posterior median hooklet-bearing lobes, and much better developed bundles on each side running anteriorly to beyond the neck region of the haptor.



Text-figs. 8–13. The hooks and supporting bars of amphibdellids, all drawn to the same scale. A, ventral hooks; B, dorsal hooks. C, supporting bars. Figs. 8 A, B. C. *Amphibdelloides maccallumi.* Figs. 9 A, B, C. *A. vallei.* Figs. 10 A, B, C. *A narcine.* Figs. 11 A, B. *Amphibdella flavolineata.* Figs. 12 A, B. *A. torpedinis.* Figs. 13 A, B. *A. paronaperugiae.* (Figs. 10 A, B after Hargis, 1955.)

Posterior glands

At the posterior end of the body of *Amphibdelloides maccallumi*, between the posterior regions of the vitellaria and the hooks of the adhesive apparatus, is a prominent mass of gland cells (Text-fig. 1). Posteriorly some extensions from the gland flank the large hooks of the adhesive apparatus and probably lead one to each of the two posterior median hooklet-bearing lobes.

There is no trace whatsoever, in whole specimens or in sections, of a corresponding gland in either juveniles or adults of *Amphibdella flavolineata*, but well-developed glands are present in *A. torpedinis* and *A. paronaperugiae*. A prominent posterior gland is also present in *Amphibdelloides vallei* but Hargis (1955) did not report a posterior gland in *A. narcine*, nor have I been able to find one in Hargis's specimens.

The gland cells have coarsely granular contents that readily take up carmine stains and acid dyes such as light green, aniline blue, and xylidine ponceau; they give a strongly positive result when treated with the periodic acid-Schiff test for polysaccharides. Because of its topographical situation, the gland appears likely to play a part in the attachment of the parasite to its host. If this be so, the secretion of the gland might either histolyse the host tissues or act as a cement. However, in sections of *A. maccallumi* attached to *Torpedo nobiliana* (Pl. II, fig. 1) the host epidermis, though stretched and compressed, showed no signs of erosion apart from the perforations made by the large hooks themselves; nor was any cement substance to be seen between the parasite and host tissues though such cement, if present in living parasites, could of course have been removed by histological processing.

ANTERIOR GLANDS

At the anterior end of *Amphibdelloides maccallumi*, and opening on to the three pairs of papillae on the anterio-lateral borders of the parasite, are some well defined anterior glands (Text-fig. 14). Their function is not known, but presumably it is either adhesive (to keep the mouth in a feeding position) or histolytic (to soften host tissues to permit ingestion).

Exactly similarly disposed glands are present in *A. vallei* and *A. narcine*, but in all three species of *Amphibdella*, namely, *A. flavolineata*, *A. torpedinis*, and *A. paronaperugiae*, there are no papillae and the openings of the ducts of the glands nearly always converge to form a single mass on each side of the body (Text-fig. 15). In a sample of ten balsam-mounted preparations of *A. flavolineata* a subdivision into three tracts of ducts could be recognized on one side only of each of two specimens, and in one living specimen examined especially for this character, there was no trace of subdivision within the paired masses of anterior glands. The same situation occurs in *A. torpedinis*, but I have found no evidence of any subdivision at all in the paired anterior glands of *A. paronaperugiae*. Ruszkowski (1931, fig. 1) illustrated a single mass of 'cephalic glands' in parasites from *Torpedo torpedo* which he called *Amphibdella torpedinis* but which the present study shows to belong to the new species *A. paronaperugiae*.

GENITALIA

Male (Text-figs. 14–22)

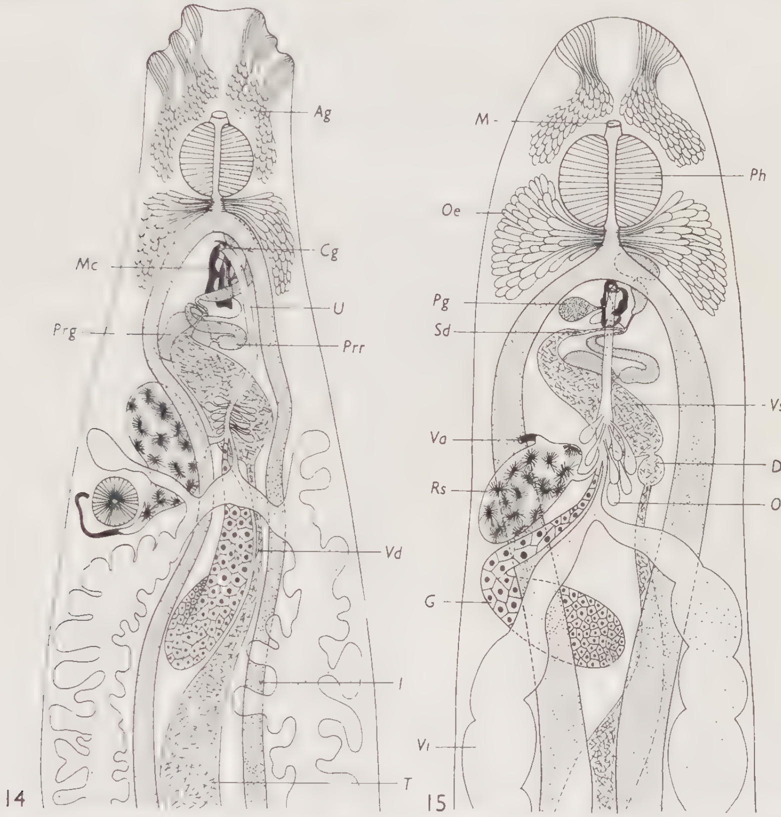
In all of the six species of amphibdellid studied there is a single testis (*T*) lying between the two intestinal limbs in the mid-dorsal region of the body, and extending posteriorly almost to the posterior ends of these intestinal limbs. Anteriorly the testis gives rise to the vas deferens (*Vd*) which passes obliquely forwards, towards the animal's left, to the posterior end of the vesicula seminalis (*Vs*). In *Amphibdelloides* the undifferentiated vas deferens enters the vesicula seminalis directly, but in *Amphibdella* a well developed and characteristic dilatation of the vas deferens (*Dvd*) is present immediately posterior to the vesicula seminalis.

The vesicula seminalis is a prominent organ with walls provided with well developed longitudinal and transverse muscle fibres that may be seen especially easily in living specimens examined in polarized light. The vesicula seminalis passes obliquely forwards from the animal's left towards the right, and at its anterior end gives off a sperm duct (*Sd*) which passes towards the left. This sperm duct then receives two ducts, one from each of the two prominent 'prostate' reservoirs (*Prr*) and the union of all three ducts has common and direct access to the slightly expanded base of the sclerotized penis which curves away anteriorly. Each prostate reservoir is connected by a short and very narrow duct (2–3 μ in diameter) with a relatively large 'prostate' gland (*Prg*). The disposition of the two prostate reservoirs (which, in whole specimens, are much more prominent than their associated glands), one anterior and the other posterior to the junction of the sperm duct with the penis, is characteristic of the family.

The copulatory apparatus consists of a very long slender sclerotized penis accompanied by a pair of relatively very large robust accessory sclerites which resemble somewhat a pair of pincers. This apparatus lies in the sagittal plane of the parasite with its proximal, posterior end lying dorsally in the body and with its long axis sloping anteriorly and ventrally so that the penis emerges on the ventral surface of the body. Its detailed structure may be seen only in well-flattened and consequently distorted specimens, and is best studied when dissected from fresh or partly decomposed specimens.

In both *Amphibdella* and *Amphibdelloides* (Text-figs. 16–21) there is a single-pointed strongly curved hook-like accessory sclerite on the parasite's left, and a differently shaped accessory sclerite on the right. In *Amphibdella* this right sclerite is a tube with an open trumpet-shaped distal end, but in

Amphibdelloides it is a hook. In *A. maccallumi* this hook bears five prongs lying in different planes so that it is only rarely that all five may be seen in one specimen. While the function of the combined pair of accessory sclerites is probably identical in *Amphibdella* and *Amphibdelloides*, namely, to act as a pair of pincers to grasp the vaginal region of the co-copulant and so to facilitate the insertion of the slender penis, nevertheless, there is a great difference in the division of labour between the two members of the pair of accessory sclerites in the two genera. In *Amphibdelloides* the single-hooked sclerite of the left (*Ps*) is perforated to carry the penis, with the hook of the right serving as the opposable pincer (*Os*), whereas in *Amphibdella* it is the trumpet-like

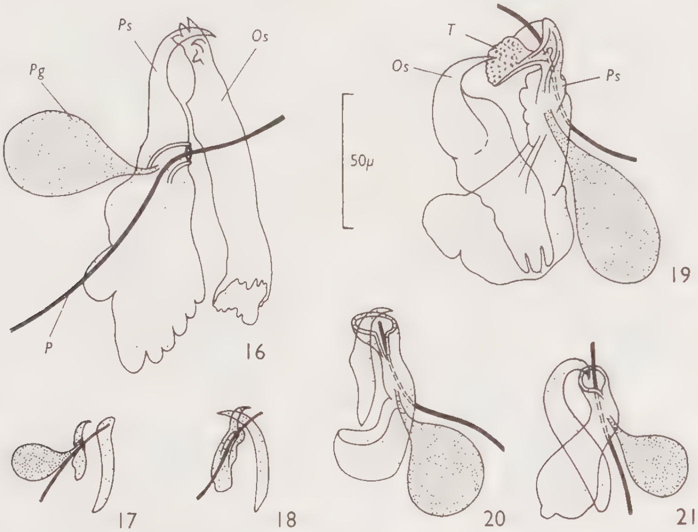


Text-figs. 14, 15. Genitalia and anterior glands of amphibdellids. Fig. 14. *Amphibdelloides maccallumi*. Fig. 15. *Amphibdella flavolineata*. *Ag*, anterior gland; *Cg*, common genital opening; *Dvd*, dilatation of vas deferens; *I*, intestine; *G*, germarium; *M*, mouth; *Mc*, male copulatory apparatus; *Oe*, oesophageal glands; *Og*, ootype glands; *Pg*, penis gland; *Ph*, pharynx; *Prg*, 'prostate' gland; *Prr*, 'prostate' reservoir; *Rs*, receptaculum seminis; *Sd*, sperm duct; *U*, uterus; *Va*, vagina; *Vd*, vas deferens; *Vi*, vitellarium; *Vs*, vesicula seminalis; *T*, testis.

sclerite of the right side which acts as the penis-bearer (*Ps*) and the single-hooked sclerite of the left as the opposable sclerite (*Os*).

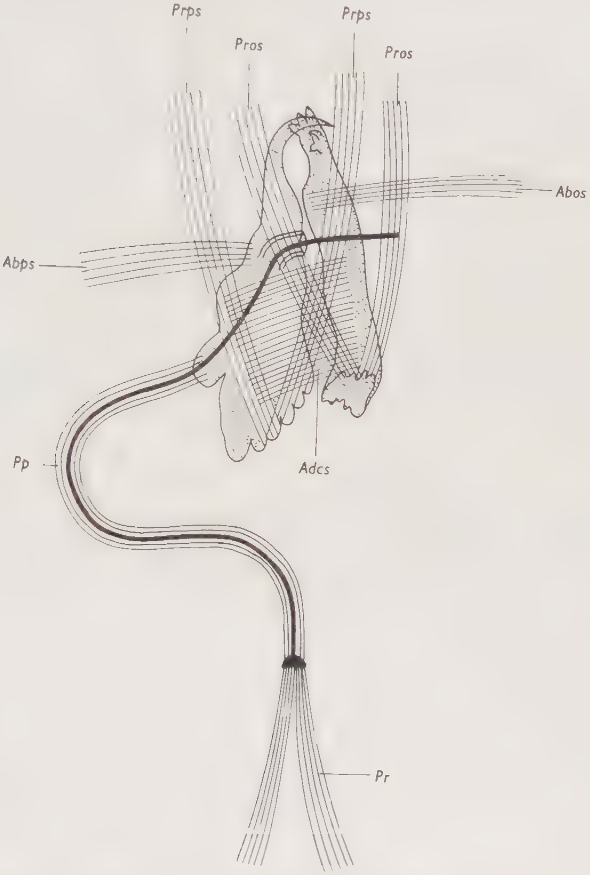
At the point of entry of the penis into the penis-bearing sclerite, this sclerite in all species of both genera (excepting *Amphibdelloides narcine*) whether it be hooked and on the parasite's left or trumpet-shaped and on the parasite's right, receives the duct of a very prominent 'penis gland' (*Pg*).

Within each of the two genera *Amphibdelloides* and *Amphibdella* the specific differences in the male copulatory apparatus are mainly of size, as illustrated in Text-figs. 16–21. In *Amphibdella*, however, there is a further difference in that while the distal end of the penis-bearing sclerite of *A. flavolineata* has a prominent tubercled 'lower-lip' region (*T* in Text-fig. 19), such a feature is absent from *A. torpedinis* (Text-fig. 20) and *A. paronaperugiae* (Text-fig. 21). In *Amphibdelloides narcine*, Hargis (1955) did not report, nor have I been able to find, a penis gland. Again in *A. narcine* the accessory sclerites were described by Hargis as being only 18–31 μ in length, but in well-flattened specimens, or in specimens in which the copulatory sclerites can be seen in side view, I have found the opposable sclerite to be 37 (36–40) μ long.



Text-figs. 16–21. Male copulatory apparatus of amphibdellids in dorsal view, all drawn to same scale. Figs. 16–18. *Amphibdelloides*: Fig. 16. *A. maccallumi*. Fig. 17. *A. vallei*. Fig. 18. *A. narcine*. Figs. 19–21. *Amphibdella*. Fig. 19. *A. flavolineata*. Fig. 20. *A. torpedinis*. Fig. 21. *A. paronaperugiae*. *Os*, opposable sclerite; *P*, penis; *Pg*, penis gland; *Ps*, penis-bearing sclerite; *T*, tubercled lip region of penis-bearing sclerite of *Amphibdella flavolineata*.

The copulatory apparatus of amphibdellids is provided with various muscles, the most prominent of which are indicated in Text-fig. 22, which was constructed from observations of whole mount specimens of *A. maccallumi* seen in polarized light. Smaller muscles, which appear to be antagonists to some of the larger ones included in Text-fig. 22, are also present, but they have been omitted from the diagram to reduce confusion. A special hazard in the determination of the distribution of the muscles of the copulatory apparatus was the presence of sphincter muscles (not shown in Text-fig. 22) surrounding the opening of the genital atrium and lying immediately ventral to the distal ends of the copulatory sclerites.



Text-fig. 22. The male copulatory apparatus of *Amphibdelloides maccallumi*, accessory sclerites somewhat displaced to permit illustration of muscles. *Abos*, abductor of opposable sclerite; *Abps*, abductor of penis-bearing sclerite; *Adcs*, adductor of copulatory sclerites; *Pp*, protractors of penis; *Pr*, retractors of penis; *Pros*, protractors of opposable sclerite; *Prps*, protractors of penis-bearing sclerite.

The copulatory apparatus has not been seen working, but from a consideration of the spatial relationships between the various parts in *A. mac-*

callumi it seems likely that its mode of action is as follows. With the distal end of the penis still contained within the penis-bearing sclerite, the distal ends of the two copulatory sclerites are extruded through the opening of the common genital atrium by the contraction of the protractor muscles, of which each copulatory sclerite has a pair (*Pros*, *Prps*). Next the abductor muscles (*Abos*, *Abps*) pull apart the distal ends of the copulatory sclerites as a preliminary to the grasping of the vaginal region of the body of the co-copulant, an action which is brought about by the contraction of the proximally situated adductor muscles (*Adcs*) and a corresponding relaxation of the abductor muscles (*Abos*, *Abps*). Finally, there is a contraction of the loose sleeve of protractor muscles (*Pp*) surrounding the long, slender, curved sclerotized but flexible penis; these muscles connect the sclerotized disc at the proximal end of the penis with the penis-bearing copulatory sclerite, and their contraction would result in the protrusion of the distal end of the penis. Such action would resemble somewhat that of cable-operated mechanical devices, but the biological apparatus differs from engineering ones in that the power is supplied intrinsically by the sleeve or sheath being itself contractile and fixed at one end to the proximal end of the axial cable-like penis.

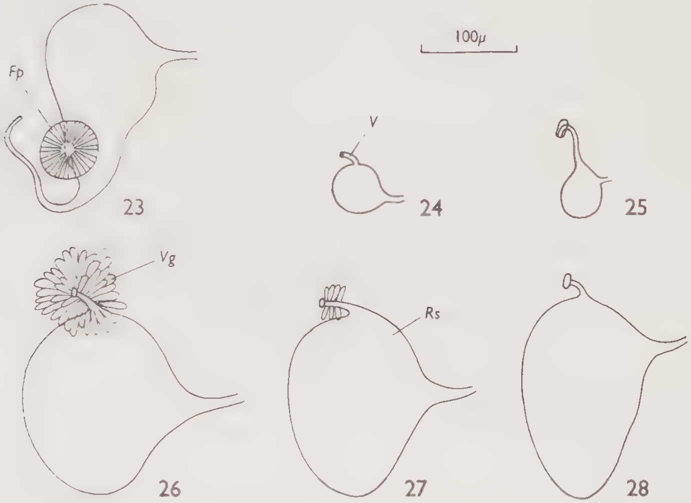
Female (Text-figs. 14, 15, and 23–28)

The general plan of the female genitalia in amphibdellids is as shown in Text-figs. 14 and 15, and here attention will be drawn only to the differences between *Amphibdelloides* and *Amphibdella* and to the specific variations within the two genera.

The germarium in *Amphibdelloides* lies approximately in the sagittal plane of the parasite, with no part of it lateral to the intestinal limbs and vitellaria. In *Amphibdella*, however, the germarium makes a lateral loop which passes first dorsal to the intestinal limb and vitelline tract of the right side of the body, then turns ventrally outside these organs, finally to curve medially to pass ventrally to them before regaining a position in the sagittal plane of the body.

In five of the six species of amphibdellid studied the vitellarium was found to be follicular (*Vi* in Text-fig. 14) like that of the vast majority of monogeneans, but in *A. flavolineata* the vitellarium was found to consist of two long tubes exhibiting only a very slight degree of lobing. Paraffin sections of *A flavolineata* showed no trace of a follicular organization inside the vitellarium.

In *Amphibdelloides* the vagina opens on the dorso-lateral surface of the body, but in *Amphibdella* it opens on the ventro-lateral surface. Within each of the two genera, the main variations in the female genitalia are as follows: differences in the length of the sclerotized vagina; variations in the site of origin of the vagina from the receptaculum seminis; differences in the form of the distal end of the vagina, whether a simple tube or whether provided with an expanded sclerite; the presence or otherwise, and the degree of development of, a vaginal gland; and the size, and sometimes the shape, of the receptaculum seminis. With regard to the last character, it must be pointed out that in most species the receptaculum seminis in life is probably spherical, but that it suffers considerable change when specimens are flattened. In *Amphibdelloides maccallumi*, however, the receptaculum seminis is characteristically pyriform with the narrow end directed posteriorly. Moreover, a special organ ('fibrous pad') is present in this species, and will be described below. The particular form of the female copulatory apparatus in the various amphibdellids is illustrated in Text-figs. 22–28, and will be referred to in the specific diagnoses on pp. 580–2.



Text-figs. 23–28. Female copulatory apparatus of amphibdellids in dorsal view, all drawn to same scale. Figs. 23–25. *Amphibdelloides*. Fig. 23. *A. maccallumi*. Fig. 24. *A. vallei*. Fig. 25. *A. narcine*. Figs. 26–28. *Amphibdella*. Fig. 26. *A. flavolineata*. Fig. 27. *A. torpedinis*. Fig. 28. *A. paronaperugiae*. *Fp*, fibrous pad; *Rs*, receptaculum seminis; *V*, vagina; *Vg*, vaginal gland.

Near to the vaginal opening in *A. maccallumi* there is a thick disc of fibrous tissue simulating somewhat the appearance of a sucker (Text-figs. 14, 23). In this disc the fibres are arranged perpendicularly to the body surface of the parasite, but they are not bounded from the underlying tissue by a basement membrane. Moreover, there appears to be no trace of a concavity on the outer surface of the organ such as is present in ordinary acetabulate suckers. It is necessary to point out too that this fibrous disc lies to one side of (and so does not surround) the vaginal opening as it was described to do so by Alexander (1954) in *A. maccallumi* from *Torpedo californica*. The fibrous disc is not easily seen in whole specimens except when observed by phase contrast microscopy, but it is readily seen in sections (Pl. II, fig. 1 on the dorsal surface of the parasite, one-quarter of the length of the animal from the anterior end). Dr Alexander was kind enough to lend me some of his specimens of *A. maccallumi* from *Torpedo californica*, and I have confirmed that the position of the fibrous disc in these specimens is the same as in Plymouth specimens of *Amphibdelloides maccallumi*. There is no trace of a corresponding organ in the other amphibdellids studied.

If the fibrous disc is in fact a sucker, then its special function would appear to be that of attaching the vaginal region of the parasite to the genital atrial region (i.e. the region of the extruded accessory copulatory sclerites) of the co-copulant. But if the organ is not a sucker, as indeed seems the more likely, then it is possible that it serves as a 'toughened pad' which may be gripped firmly by, and even be perforated by, the accessory sclerites of the co-copulant with a reduced risk of damage to underlying organs such as the gut or vitellarium.

It is noteworthy that in both *Amphibdelloides* and *Amphibdella* the sperms in the receptaculum are not randomly distributed as they are in the vesicula seminalis; instead they are aggregated around spherical or elongated masses of an acidiphilic substance (Text-figs. 14, 15). The walls of the receptaculum seminis are not glandular, and the inference is that the acidiphilic substance has come from elsewhere; if this be so, then a possible source would be the 'prostate' gland of a co-copulant.

STATUS OF BLOOD-LIVING AMPHIBDELLIDS

The amphibdellids collected from the hearts of electric rays were examined carefully in respect of all of the characters which have been found to vary in the different species of the family. It was found that specimens from the heart of *Torpedo nobiliana* were very similar to specimens of *Amphibdella flavolineata* from the parietal mucosa of the gills of the same host, differing only in their smaller size, in the absence of enlarged hooklet-bearing lobes, in the absence of vitellaria, and in the presence of only a rudimentary germarium. The size and shape of the accessory sclerites of the male copulatory apparatus, including the tubercled trumpet-shaped opening of the penis-bearing sclerite, was identical in the blood stream and gill mucosa forms, as also were the position of the ventrally opening vagina anterior to the receptaculum seminis, the presence of a dilatation in the vas deferens immediately preceding the vesicula seminalis, the shape of the large hooks, and the absence of a transverse bar and a posterior gland.

An almost parallel situation was present in the amphibdellids from the heart of *Torpedo marmorata*, but here a rudimentary posterior gland was present, and the shape and size of the hooklet-bearing lobes of the haptor was as in *Amphibdella torpedinis* from the parietal mucosa of the gills.

It is noteworthy that in the amphibdellids from the hearts of both *Torpedo nobiliana* and *T. marmorata*, while the female gonads were invariably undeveloped, in all specimens examined the vesicula seminalis was full of sperms showing that the testis was already functional. Moreover, the receptaculum seminis was invariably well filled with sperms, indicating that copulation had probably taken place.

The obvious inference is that these amphibdellids from the blood systems of their hosts are 'juvenile' specimens of the *Amphibdella* species which attaches itself to the gill mucosa of the particular host species. The blood parasites are juvenile in that the female genitalia are as yet immature, but the male genitalia are already mature. An alternative view would be to regard the blood-living parasites as protandrous adults.

The advantage of a protandrous stage living freely in the blood stream would be in the greatly improved opportunities for meeting a partner and so of permitting cross-fertilization to take place. Copulation between gill specimens permanently anchored in the subcutaneous tissues of the host would be restricted to those specimens happening to lie very near to each other. Such a distribution has been observed occasionally in *A. torpedinis*, but in none of the specimens of *A. flavolineata* that I have collected from the gills would copulation have been possible.

The life-cycle of species of the genus *Amphibdella* then would appear to be as follows. Free-living sixteen-hooked oncomiracidia encounter the appropriate torpedinid host and, instead of settling permanently on the superficial gill tissues as other monogenean gill parasites are thought to do, penetrate into the blood vessels of the gills. The larva is carried around in the blood stream and develops until eventually it exchanges sperms with a co-copulant. It would then emerge, anterior end first, through the gill mucosa (the parasite being too big to enter the capillaries of the secondary lamellae), thus exposing the uterine aperture for oviposition, and with the posterior end remaining within the host tissues. It seems unlikely that the parasite would emerge completely and then re-insert the posterior end of its body into the host, for there appears to be no boring apparatus present; 'posterior glands' of uncertain function are indeed present in *A. torpedinis* and *A. paronaperugiae* but are absent from *A. flavolineata*. Ruszkowski (1931) found egg-laying specimens and free egg capsules of *A. paronaperugiae* in the blood system of *Torpedo torpedo*; but he also reported (p. 163) individuals of the same species as living on the gills; it is possible that the egg-capsules in the blood system were merely an example of precocious egg-laying.

TAXONOMY

The preceding comparisons of amphibdellids from various micro-habitats on various torpedinid host species have made necessary certain taxonomic revisions; these are given below.

Family: AMPHIBDELLIDAE Bychowsky, 1957 emend.

Tetraonchidea (Bychowsky, 1957) with bifurcate but otherwise unbranched intestine; adults with two pairs of large hooks, with or without a single supporting bar; sixteen persistent oncomiracidial hooklets arranged as five lateral pairs including four marginal pairs and one submarginal pair, and two median pairs including one posterior terminal pair and one centrally placed pair; eyes absent in oncomiracidium and adult; adults parasitic on secondary gill lamellae or gill mucosa of Torpedinidae, but juveniles of some species endoparasitic in blood system of host. Type genus: *Amphibdella* Chatin, 1874.

The above family diagnosis differs from that given by Bychowsky in that it recognizes that the supporting bar is absent from half of the known species, and in that it gives more details about the distribution of persistent oncomiracidial hooks in the adult, and about the micro-habitats of the parasites. Since the type genus is *Amphibdella*, the family name should be Amphibdellidae not 'Amphibdellatidae' as given by Bychowsky.

Genus: **Amphibdella** Chatin, 1874

Amphibdellidae without transverse bar supporting the large hooks; posterior gland present or absent; germarium loops around right intestinal limb; vitellarium follicular or tubular; vaginal opening on ventro-lateral surface of body; with or without vaginal gland; vagina arising from anterior end of receptaculum seminis; with dilatation in vas deferens immediately preceding vesicula seminalis; right male copulatory sclerite trumpet-shaped and serving as penis-bearer, left male copulatory sclerite with terminal hook; adults parasitic on mucosa of gills, but some development, involving protandry, takes place in blood system of host. Type species: *Amphibdella torpedinis* Chatin, 1874.

Amphibdella torpedinis Chatin, 1874

Length 4·45 (3·20–5·68) mm, width 0·68 (0·60–0·80) mm; haptor not separated from remainder of body by a narrow neck; hooklet-bearing lobes not greatly enlarged; large hooks 155 (136–172) μ long, of characteristic shape illustrated in Text-figs. 12A, B and lacking a distinct shoulder at the junction of the broad flattened part with the curved slender part; with posterior gland; penis-bearing copulatory sclerite 64 (60–78) μ long and with smooth trumpet; vaginal gland poorly developed; distal end of vagina slightly swollen to about 8–10 μ external diameter; parasites of gill mucosa of *Torpedo marmorata* with part of juvenile development in blood system of same host.

Amphibdella paronaperugiae sp.nov.

Length 3·82 (2·60–4·80) mm, width 0·37 (0·24–0·46) mm; large hooks 138 (132–148) μ long, with distinct shoulder at junction of broad flattened part with curved slender part as illustrated in Text-figs. 13A, B; vaginal gland absent; distal end of vagina swollen to 12–16 μ external diameter; penis-bearing copulatory sclerite 54 (48–58) μ long; parasites of gill mucosa of *Torpedo torpedo*, but some egg-laying adults, probably precociously developed, have been reported from the blood system of the host. Other characters as in *Amphibdella torpedinis*.

Amphibdella flavolineata MacCallum, 1916

Length 4·85 (3·20–6·60) mm, width 0·75 (0·40–1·20) mm; haptor separated from remainder of body by a narrow neck; two median pairs of hooklet-bearing lobes greatly expanded; large hooks 156 (152–160) μ long and lacking distinct shoulder at junction of broad flattened part with curved slender part as illustrated in Text-figs. 11A, B; without posterior gland; vitellarium tubular and not follicular; penis-bearing copulatory sclerite 102 (96–116) μ long with tubercled lip to trumpet as illustrated in Text-fig. 19; with very well-developed vaginal gland; distal end of vagina only very slightly swollen to about 6–8 μ external diameter; parasites of gill mucosa of *Torpedo nobiliana*, with part of juvenile development in blood system of same host.

Genus: **Amphibdelloides** Price, 1937

Amphibdellidae with transverse bar supporting the large hooks; posterior gland present; germarium lying entirely within the intercaecal field; vitellarium always follicular; vagina opening on dorso-lateral surface of the body; without vaginal gland; vagina arising from anterior or posterior end of receptaculum seminis; without dilatation in vas deferens; left copulatory sclerite hook-shaped and serving as penis-bearer, right copulatory sclerite another hook, sometimes with terminal prongs; adults parasitic on secondary gill lamellae of hosts, juvenile development not known. Type species: *Amphibdelloides maccallumi* (Johnston & Tiegs, 1922) Price 1937.

Amphibdelloides maccallumi (Johnston & Tiegs, 1922) Price, 1937

Length 2·66 (2·00–3·00) mm, width 0·45 (0·32–0·58) mm; large hooks 172 (160–194) μ long, of characteristic shape illustrated in Text-figs. 8A, B and supported by a transverse bar 79 (72–84) μ long; with fibrous pad near vaginal aperture; vagina arising from posterior end of receptaculum seminis and ending in a simple tubular opening; receptaculum seminis pyriform with narrow end directed posteriorly; penis-bearing copulatory sclerite 140 (130–160) μ long; parasitic on *Torpedo nobiliana* and *T. californica*.

Amphibdelloides vallei sp.nov.

Length 0·86 (0·60–1·20) mm, width 0·14 (0·10–0·24) mm; large hooks 100 (92–104) μ long, of characteristic shape illustrated in Text-figs. 9A, B and supported by a transverse bar 44 (42–48) μ long; without fibrous pad near vaginal opening; vagina arising from anterior end of receptaculum seminis and ending in a simple tubular opening; receptaculum seminis spherical; penis-bearing copulatory sclerite 37 (35–38) μ long; parasitic on *Torpedo marmorata*.

Amphibdelloides narcine Hargis, 1955 (diagnosis based mainly on Hargis, 1955)

Length 0·90 (0·79–1·87) mm, width 0·16 (0·15–0·19) mm; large hooks 97 (85–108) μ long, of characteristic shape illustrated in Text-figs. 10A, B and supported by a transverse bar 35 (26–51) μ long; without fibrous pad near vaginal opening; vagina arising from anterior end of receptaculum seminis and ending in a sclerotized plate about 18 (16–20) μ long by 10 (8–12) μ wide (in the illustration of the sclerotized plate of the vagina by Hargis, 1955, fig. 18, the scale is erroneously magnified by a factor of about 5); receptaculum seminis slightly pyriform with narrow end directed anteriorly; penis-bearing copulatory sclerite 37 (36–40) μ long (see p. 574); parasitic on *Narcine brasiliensis*.

Other species of the Amphibdellidae

Both Monticelli (1890) and Ruszkowski (1931, footnote to p. 164) have referred to what is likely to be a new species of *Amphibdelloides* from the secondary gill lamellae of *Torpedo torpedo*.

Bychowsky (1957) has referred to an amphibdellid from the gills of *T. smithi* from the Arabian Sea, Baluchistan.

I have had an opportunity of seeing a new species of *Amphibdella* from the gills of *Narcine timlei* from South India; this amphibdellid was found by and will be described by Mr R. V. Unnithan.

On the basis of the above classificatory scheme, it is now proposed to review the taxonomic histories of the various amphibdellid species.

The first monogenean from an electric ray was described by Chatin (1874) as *Amphibdella torpedinis* (without a transverse bar in the adhesive apparatus) and was collected from the gills of *Torpedo marmorata* at Naples. Chatin's description was vague and inaccurate, and a more detailed diagnosis of the species, based on specimens collected from the same host species at Sète (Mediterranean, Gulf of Lyons), is given in the present paper.

Monogeneans were also found on this same host *T. marmorata* at Trieste by Valle, who sent the parasites to Genoa, where they were described by Perugia and Parona (1890) under the name of '*Amphibdella torpedinis* Chatin'. Valle's specimens were said to have one transverse bar in the adhesive apparatus, but in a later paper (Parona & Perugia, 1890) this observation was qualified: it was now stated that there were really two bars present, one of them having been omitted from the illustration in the earlier paper for the sake of simplicity. In describing two bars as being present, however, Parona & Perugia were almost certainly mistaken: as pointed out by Bychowsky (1957), what was thought to be the second transverse bar was very probably the muscle connecting the anterior ends of one of the pairs of hooks. A corresponding muscle (*Bm*) in *Amphibdelloides maccallumi* is illustrated in Text-fig. 7. This second amphibdellid (with one transverse bar) from *Torpedo marmorata* has been designated in the present study a new species *Amphibdelloides vallei*.

Following their description (written in November 1889) of Valle's amphibdellids from *Torpedo marmorata*, Parona and Perugia (1890) themselves collected and described in April 1890 some monogeneans from *T. torpedo* (syn. *T. narce*) at Genoa. These parasites were collected not from the gill lamellae, but from the parietal mucosa of the gill chamber, and were found to be without a transverse bar. Though Parona & Perugia described the parasites from the parietal mucosa of *T. torpedo* as *Amphibdella torpedinis* Chatin, their specimens (from the C.E.C.I., Naples) have been re-examined in the course of the present study and were found to belong in fact to a new species (without bar) for which the name *A. paronaperugiae* has been proposed. The same species was collected from the gills of *Torpedo torpedo* (syn. *T. ocellata*) at Naples by Ruszkowski (1931, p. 163), and also from the heart and urinogenital system of this host, the specimens being identified by Ruszkowski as Chatin's '*Amphibdella torpedinis*'.

At about the same time that Parona & Perugia discovered the amphibdellid *without* a transverse bar on the parietal mucosa of the gills of *Torpedo torpedo* at Genoa, Monticelli (1890) recorded under the name of '*Tetraonchus torpedinis* Chatin' what is probably a second species (*with* a transverse bar) from the same host species *Torpedo torpedo* (syn. *T. narce*) at Naples; this same species was probably recorded again from the same host *T. torpedo* (syn. *T. ocellata*) at Naples by Ruszkowski (1931, footnote to p. 164). Monticelli referred to the presence of two transverse bars, but in this he almost certainly made a mistake similar to that made by Parona & Perugia (1890) and referred to above. Thus it is highly desirable that the gills of *T. torpedo* be searched again for a second species of amphibdellid and that the parasite be described in detail.

MacCallum (1916) discovered two species of amphibdellids on the gills of *T. nobiliana* (syn. *Tetranarce occidentalis*) from Woods Hole, U.S.A., and identified one of them (*with* a transverse bar!) as Chatin's *Amphibdella torpedinis* and the other (without a transverse bar) as a new species *A. flavolineata*. Johnston & Tiegs (1922) proposed a new species *A. maccallumi* for MacCallum's specimens of '*A torpedinis*' and later Price (1937) made this species the type of a new genus *Amphibdelloides* characterized by the presence of a transverse bar. In the course of the present study MacCallum's specimens have been borrowed from the United States National Helminthological Collection and have been compared with specimens of *A. maccallumi* and *Amphibdella flavolineata* from the same host *Torpedo nobiliana* captured in Europe (Plymouth, Irish Sea, Irish Atlantic Slope, and Mediterranean), and have been found to be identical. It is concluded that Price's recognition of two distinct genera according to the presence or absence of a transverse bar is basically sound, but that Price's second character, namely, that concerning the lobing of the posterior adhesive apparatus, needs considerable modification. Such a modification, together with some new generic characters, is proposed on pp. 580–2.

Palombi (1949), in his review of trematodes from Italy, regarded all amphibdellids previously recorded from Mediterranean hosts as belonging to one species *Amphibdella torpedinis* in which a transverse bar was constantly present and distinct in small specimens, but absent from large specimens.

Recently Alexander (1954) has recorded and redescribed *Amphibdelloides maccallumi* from *Torpedo californica* from California. I have compared some of Alexander's actual specimens with MacCallum's specimens and also with specimens of *Amphibdelloides maccallumi* from *Torpedo nobiliana* (i.e. the same host species as that from which MacCallum's material was collected) from various European localities, but can find no significant differences between any of them. Then in spite of the strongly suggestive evidence from the difference in host species and the difference in geographical distribution, on morphological grounds the amphibdellids with a transverse bar from *T. californica* and *T. nobiliana* must both be recognized as *Amphibdelloides maccallumi*. The inference from this parasitological evidence is that the divergence between *Torpedo californica* and *T. nobiliana* took place very recently, and support is thus given to the view of Fraser-Brunner (1949) who placed both *T. nobiliana* and *T. californica* in the subgenus *Tetronarce*, whereas *T. torpedo* and *T. marmorata* were regarded as belonging to the subgenus *Torpedo*.

Hargis (1955) described a new species *Amphibdelloides narcine* from *Narcine brasiliensis* from the Gulf of Mexico, and Euzet (1957) described the oncomiracidium of what he regarded at that time as *Amphibdelloides maccallumi* from the gills of *Torpedo marmorata* and *T. nobiliana* but which the present study has shown might properly belong either to *A. maccallumi* or to the new species *A. vallei*.

Bychowsky (1957) in surveying the systematics of the Monogenea, found previous work on amphibdellids to be inaccurate and contradictory, and in an attempt to clear up the confusion, studied specimens, some of them living, from *Torpedo marmorata*, *T. torpedo* (syn. *T. ocellata*), *T. californica* and *T. smithi*. He confirmed the observations of Ruszkowski and Palombi that there were sixteen hooklets on the haptor, and properly emphasized the phylogenetic significance of this observation. But Bychowsky refuted Price's (1937) recognition of two amphibdellid genera separated from each other by the presence or absence of a transverse bar and by the lobed or unlobed condition of the haptor, claiming that a transverse bar was always present but that it may be inconspicuous in older specimens, and that the lobing of the haptor could be greatly affected by histological fixation. The present study of the functional morphology of the adhesive apparatus has shown that the transverse bar is an integral part of the adhesive apparatus of those amphibdellids which hook themselves to secondary gill lamellae, and that it is absent from those amphibdellids which 'root' themselves subcutaneously in the gill mucosa. Thus Price's view that the presence or absence of the transverse bar was of taxonomic significance was well-founded. At the same time the present study agrees with Bychowsky's rejection of the second generic character used by Price, namely, the alleged unlobed condition of the haptor in *Amphibdelloides*. In place of Price's recognition of two genera of *Amphibdellidae* based on two characters (one of which was mis-interpreted), and of Bychowsky's recognition of a single genus, the present study accepts the same two genera as those accepted by Price, but on a basis of at least six contrasting characters, only one of which had been used by Price.

PHYLOGENY

On the basis of the above comparative morphological and taxonomic studies of the Amphibdellidae it is proposed now to speculate on the probable lines of evolutionary development within the group.

On the grounds of the very widespread occurrence of modern Tetraonchideans on the secondary gill lamellae of their hosts it may be assumed that the ancestral amphibdellid lived in a similar micro-habitat. It was attached to its host by a haptor provided with sixteen hooklet-bearing lobes, a posterior gland, and two pairs of unsupported hooks (i.e. without a transverse bar) operated by extrinsic muscles and tendons threaded through loops on the ventral hooks; such a haptor survives with least change in the present-day *Amphibdella torpedinis* and *A. paronaperugiae*. The male copulatory apparatus consisted of a pair of opposable sclerites, one on the left with a hook, and one on the right consisting of a simple bar, with the penis lying freely between them.

The dominating environmental hazard was the gill ventilating current of the host, and the parasite began to meet the problem in two different ways. One way was to make the hook apparatus more efficient by developing an accessory transverse supporting bar (the ancestral *Amphibdelloides*); the other was to relieve the hooks of some of their burden by 'rooting' the haptor subcutaneously in the host (the ancestral *Amphibdella*). In the second method it was an advantage to move from the relatively thin and delicate secondary lamellae to the more robust adjacent mucosa.

The dominating evolutionary trend now became towards increased efficiency of the copulatory apparatus. This took the form of a closer association of the penis with one of the accessory sclerites so that the latter acted as a guide. However, in the diverging *Amphibdelloides* and *Amphibdella* stocks different sclerites were used for the development of such a guide: in *Amphibdelloides* the left, hooked sclerite became the guide, with the penis emerging from the side of the sclerite, but in *Amphibdella* the right sclerite became tubular with the penis emerging through its distal end, the left sclerite retaining its more primitive function of acting as an opposable hook. Associated with these divergences in the male copulatory organs were some changes in the female copulatory organs: in *Amphibdella* the vaginal opening became ventro-lateral, but in *Amphibdelloides* it became dorso-lateral. Larval or juvenile forms of *Amphibdella* now took to invading the blood system of the host, perhaps to provide greater opportunities for cross-fertilization among its protandrous developmental stages (see p.579), perhaps to facilitate taking up the definitive manner of attachment (see Pl. II, fig. 2), or perhaps merely to provide a relatively sheltered environment for larval development.

At this stage there was a divergence in the host stock, on the one hand (Fraser-Brunner, 1949) into *Tetronarce* (from which the modern *Torpedo nobiliana* and *T. californica* have descended) and on the other into *Torpedo* which has given rise to the present-day *T. torpedo* and *T. marmorata*. The gills of *T. nobiliana* have become relatively large and support the relatively large parasites *Amphibdella flavolineata* and *Amphibdelloides maccallumi*, and those of *Torpedo marmorata* are relatively small and support the smaller parasites *Amphibdella torpedinis* and *Amphibdelloides vallei*.

Following this divergence in the ancestral torpedinid stock, no further speciation took place on the *Tetronarce* line of descent for a long time, and under these relatively stable conditions the amphibdelloid parasites became increasingly specialized. In *Amphibdella flavolineata* the haptor was buried more deeply in the host tissues, and some of the hooklet-bearing lobes became greatly expanded, simulating the roots of a tree in providing more efficient anchorage. The increase in the 'rooting' component of the adhesive apparatus was accompanied by a gradual decrease in the efficiency of the hook apparatus, and the muscles have become correspondingly simplified; moreover, the posterior gland was lost. While the haptor was evolving thus, the trumpet of the penis-bearing sclerite developed a roughened surface to maintain more secure coverage of the vaginal opening of the co-copulant. In *Amphibdelloides maccallumi* the main specializations were the acquisition of a fibrous pad in association with the vaginal opening, and the development of a 'catch' mechanism to lock the adductor muscles of the large hooks.

Accompanying the relatively recent speciation of the *Tetronarce* stock to give rise to the modern *Torpedo nobiliana* and *T. californica*, we would expect corresponding speciation among the amphibdellid parasites, but in the limited sample of parasites from the gill lamellae of *T. californica* there was no evidence for this; it is possible that an examination of a larger sample of fresh material from *T. californica* might reveal evidence of at least incipient speciation in *Amphibdelloides maccallumi*. No specimens of *Amphibdella flavolineata* have yet been recorded from *Torpedo californica*.

In the *Torpedo* line of host descent, speciation into *T. marmorata* and *T. torpedo* took place long enough ago to have allowed divergences to become manifest also in the amphibdellid parasites. *Amphibdella torpedinis* (without shoulders to its hooks and with a relatively simple vaginal aperture) from *Torpedo marmorata* differs from *Amphibdella paronaperugiae* (with shoulders to its hooks and with the terminal part of the vaginal sclerite enlarged) from

Torpedo torpedo. No information is available yet about the divergences which may have occurred between the corresponding *Amphibdelloides* parasites: *A. vallei* is known from *Torpedo marmorata* but the parasite from the gill lamellae of *T. torpedo* has not yet been described.

The Director and Staff of the Plymouth Laboratory have very kindly made available to me most of the rather rare electric rays brought in by the research vessels in recent years, and as always have provided excellent working facilities; Dr Louis Euzet of Sète has made special collections of specimens for me and has given me much of his own material; and the following have either arranged loans or presented me with specimens: Dr C. G. Alexander of California, Dr W. J. Hargis of Virginia, Dr M. Sara of the University of Naples, Dr H. H. Williams of Cardiff, and the United States National Museum.

SUPPLEMENTARY NOTE

In April 1960, by kind permission of Prof. P. Mathias, I was able to visit the Station Biologique at Sète, where the following observations were made.

Torpedo marmorata. (*a*) A freshly killed specimen was found to have nine very active juvenile specimens of *Amphibdella torpedinis* in its heart; these parasites were seen to move in a leech-like manner.

(*b*) Sections of the heart of a young host, prepared by and kindly shown to me by M. André Raibaut, were seen to contain a pair of juveniles of *A. torpedinis* in copulation.

Torpedo torpedo. (*a*) A single preserved specimen (caught at Sète in November 1959) was found to bear over fifty adult specimens of *Amphibdella paronaperugiae* all resembling exactly the specimens collected by Parona & Perugia and described in the paper above; all these parasites were deeply embedded in the proximal gill mucosa as described and illustrated above for *A. flavolineata*.

(*b*) In the heart of the same host specimen were three juveniles of *A. paronaperugiae*, but no adults.

(*c*) No amphibdellids were found on the secondary gill lamellae.

SUMMARY

Comparative studies of the functional morphology of the adhesive organs and the genitalia of amphibdellid parasites from various micro-habitats on five species of electric rays have resulted in the proposal of several taxonomic revisions.

The family name Amphibdellidae has been substituted for the 'Amphibdellatidae' of Bychowsky, with an amended diagnosis. Revised diagnoses have been give also for the genera *Amphibdella* Chatin and *Amphibdelloides* Price, and specific diagnoses for *Amphibdella torpedinis* Chatin, *A. flavolineata* MacCallum, *A. paronaperugiae* n.sp., *Amphibdelloides maccallumi* (Johnston & Tiegs), *A. vallei* n.sp., and *A. narcine* Hargis.

Amphibdella spp. live partly embedded subcutaneously in the gill mucosa of

their hosts, and *Amphibdelloides* spp. hooked to the secondary lamellae; there are corresponding differences in the basically complex adhesive apparatus.

There is strong evidence that juvenile development in *Amphibdella* involves a protandrous form living endoparasitically in the blood system of the host.

Speculations have been made on the phylogeny of the group.

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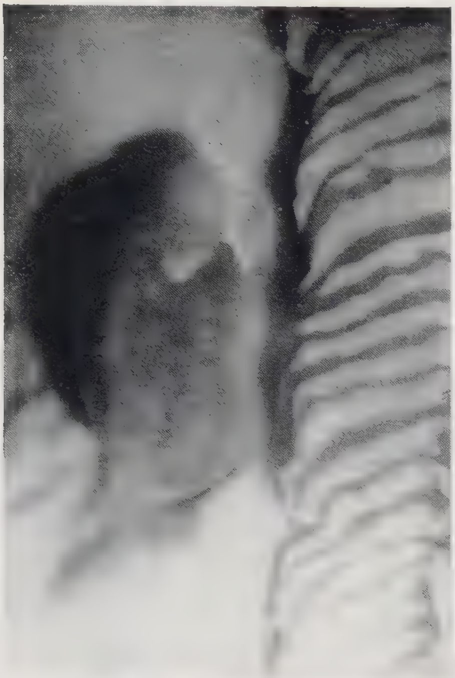

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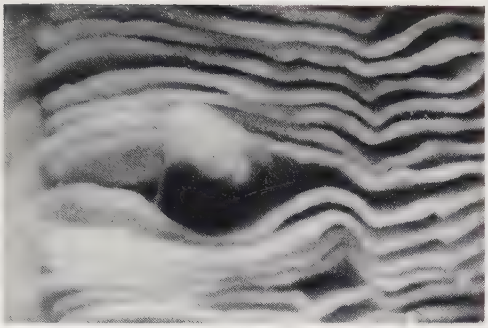

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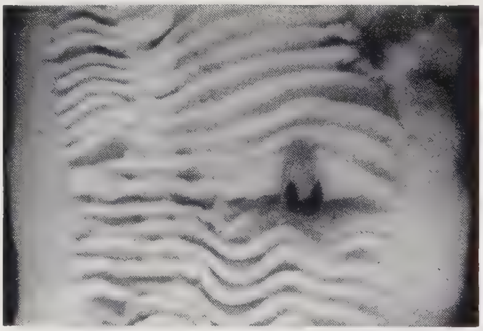

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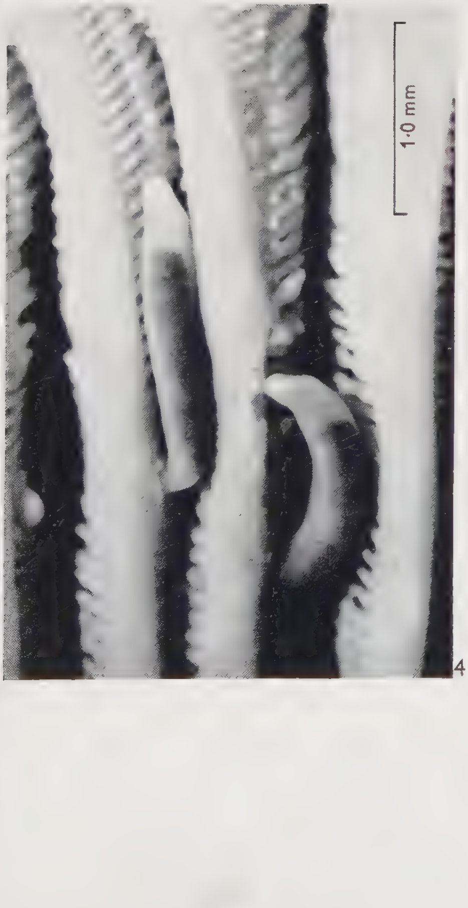

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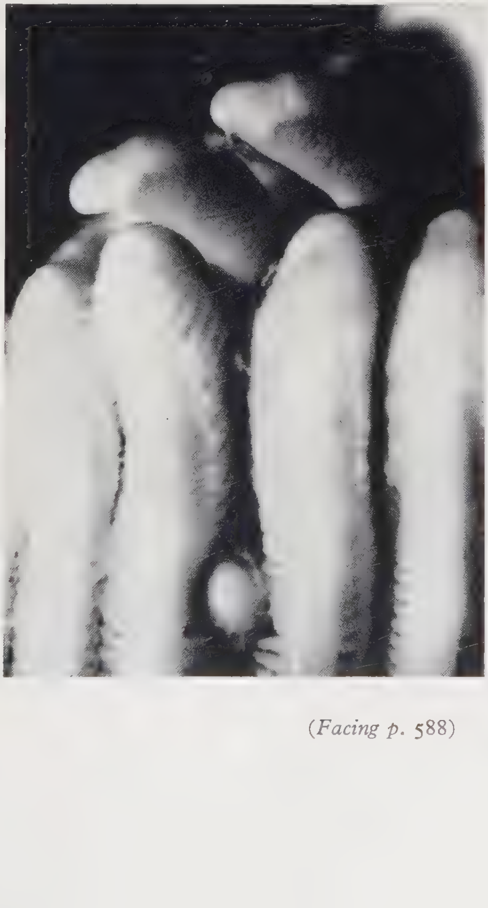

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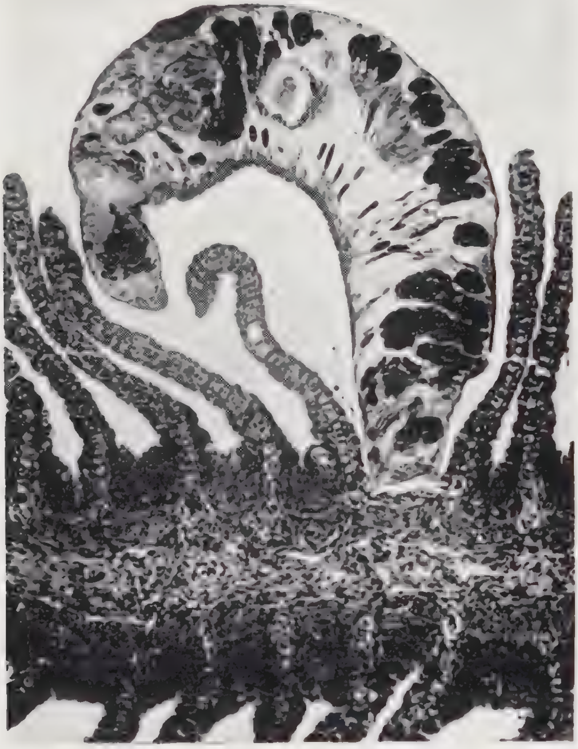

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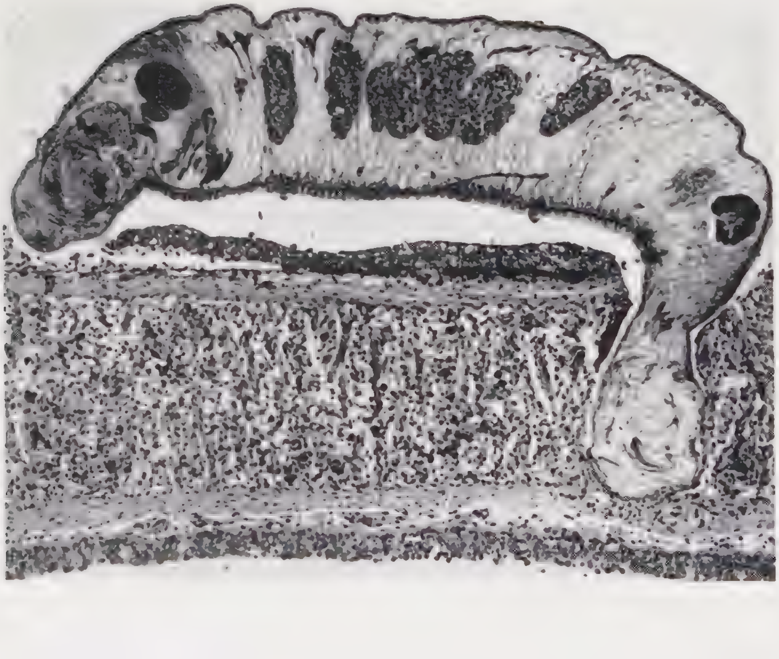

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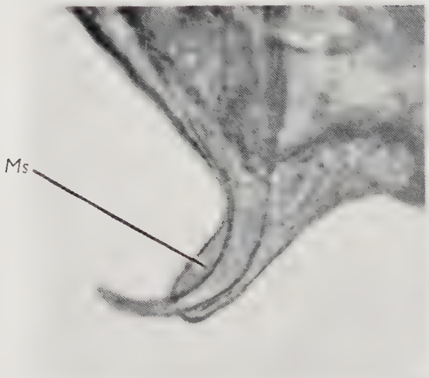
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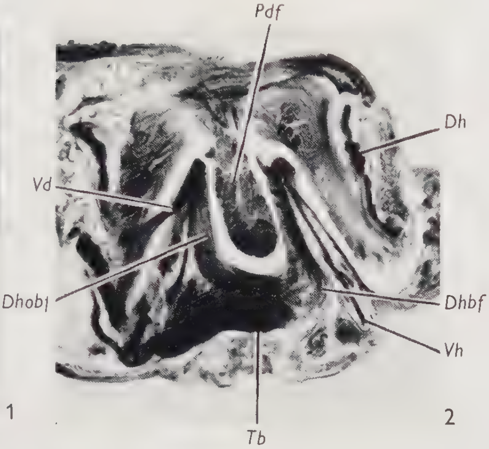
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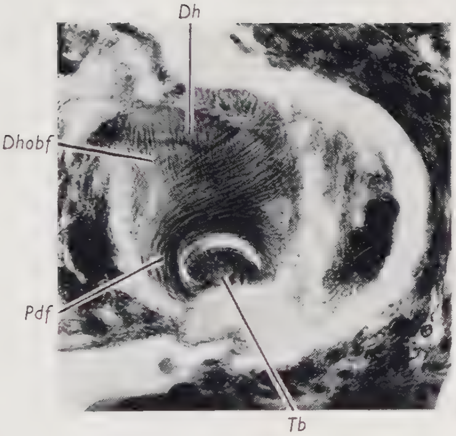
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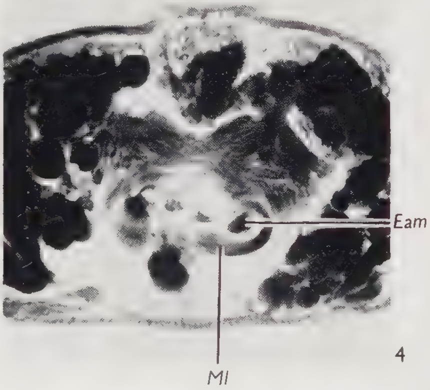
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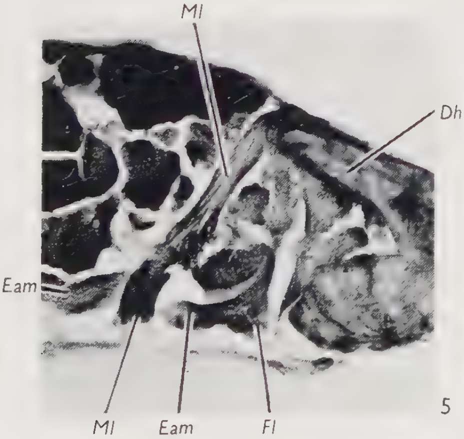
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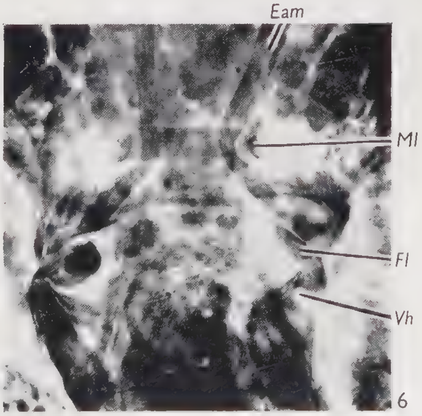
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EXPLANATION OF PLATES

Plate I

The micro-habitats of amphibdellids.

(All photographs to the same scale.)

Fig. 1. *Amphibdella flavolineata* on the gill mucosa of *Torpedo nobiliana*. Fig. 2. *Amphibdelloides maccallumi* on the secondary gill lamellae of *Torpedo nobiliana*. Fig. 3. *Amphibdelloides vallei* on the secondary gill lamellae of *Torpedo marmorata*. Figs. 4A, B. *Amphibdella torpedinis* on the gill mucosa of *Torpedo marmorata*; 4A, two specimens on the distal, free border of a primary lamella; 4B, three specimens on the proximal mucosa adjacent to the gill arch.

Plate II

The attachment of amphibdellids to their hosts.

Fig. 1. *Amphibdelloides maccallumi* hooked to the secondary gill lamellae of *Torpedo nobiliana*. Fig. 2. *Amphibdella flavolineata* 'rooted' subcutaneously in the gill mucosa of *Torpedo nobiliana*.

Plate III

The hook apparatus of *Amphibdelloides maccallumi*.

For explanation of lettering see text pp. 566–9 and compare with Text-fig. 7. Fig. 1. The muscle sheath surrounding the base of the curved part of the hook. Living specimen. Figs. 2–5. Paraffin sections of haptor. Fig. 2. Transverse section in plane of transverse bar. Fig. 3. Sagittal section. Fig. 4. Transverse section at level of median loop. Fig. 5. Parasagittal section in plane of dorsal hook. Fig. 6. Balsam preparation of whole specimen stained in chlorocarmine.

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THE EFFECTS OF SALINITY ON THE DEVELOPING EGGS AND LARVAE OF THE HERRING

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(Text-figs. 1–8)

The herring (*Clupea harengus* L.) deposits its eggs in the coastal waters around the North Atlantic Ocean, North Sea, and Baltic Sea. The salinity on the spawning grounds may vary from about 35‰ to 5‰. For instance, Brandhorst (1959) reports that successful spawning took place in the Kiel Canal in salinities down to 5‰, and Ford (1929) records that ripe herring have been found in the Tamar estuary. In a series of experiments Ford found that the eggs of herring could be successfully fertilized and incubated even in a salinity of 4·8‰. McMynn & Hoar (1953) investigated the effect of salinity on the development of the Pacific herring *C. pallasii* and found it had a wide tolerance, the lower level being somewhere between 0 and 6‰.

The experiments now described were carried out as part of an investigation into osmoregulation in the herring, and particularly to find the range of conditions which herring eggs and larvae might tolerate both in nature and in rearing tanks. An extension of this work into the temperature tolerance of herring larvae is described by Blaxter (1960).

MATERIALS AND METHODS

Ripe gonads were obtained from herring caught in the Firth of Clyde in February and off the Scottish East Coast in September and the eggs fertilized in the laboratory. The techniques of storage and fertilization are described by Blaxter (1955). After fertilization, eggs were incubated in sea water of salinity 31–32‰ at temperatures of 11·2–11·7° C in 50 l. glass tanks. Smaller numbers of larvae were incubated in water of other salinities in 500 ml. jars; the water in these jars was changed every second day. Low salinity water was made up by adding distilled water to sea water and high salinity water by adding sodium chloride to sea water.

Most of the experiments were carried out on the spring-spawned larvae while a few confirmatory ones were done in the autumn.

FERTILIZATION

Prior to fertilization both eggs and sperm normally undergo changes of environment, i.e. from the body fluids of the parent to sea water. In addition the sperm then penetrate the eggs. Thus the gametes must be resistant to osmotic stress, especially the sperm; its large surface/volume ratio and small diffusion pathways would seem to make it particularly susceptible.

To find out the tolerance of the gametes to salinity, fertilizations were carried out in salinities of 5·9, 11·5, 22·7, 33·6, 41·6, 45·0 and 52·5‰; the results are shown in Fig. 1. Fertilization was complete in salinities 22·7–52·5‰. It fell off in salinities 11·5 and 5·9‰.

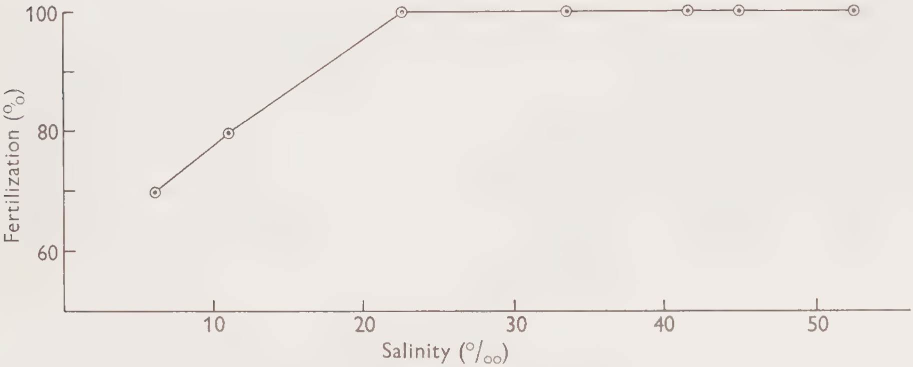

Fig. 1. Percentage fertilization of eggs.

EMBRYONIC DEVELOPMENT AND HATCHING

Krogh (1939), in a review on the subject, concludes that the developing teleost egg is not independent of the environmental salinity. In these experiments a number of observations were made to test this dependence in the herring egg.

Size of egg. The average diameter of eggs incubated in different salinities is shown in Fig. 2. It will be seen that the diameter increases in the lower salinities, due to an increase in water content.

Osmotic concentration of the eggs. Experiments were done to test whether the osmotic concentration (and therefore the proportion of water) varied in eggs incubated in different salinities. Freezing-point depressions (Δ) were determined for the perivitelline fluid and the embryonic fluid, using the apparatus described by Ramsay (1949) and Ramsay & Brown (1955).

Samples of the egg contents were taken after placing the egg under medicinal paraffin in a watch-glass coated with a lacquer of bakelite damada. A fine capillary, made of silica glass, was inserted into the perivitelline fluid and a small sample sucked in. This sample was sealed between two layers of paraffin by sucking paraffin into the capillary before and after taking the sample.

It was much more difficult to sample the body fluid of the embryo. The embryo was removed from the egg (under paraffin) and cleared of perivitelline fluid. The capillary was inserted into the posterior trunk region. Due to the difficulty of avoiding contamination with yolk many samples had to be discarded.

The results are shown in Table 1.

TABLE 1. OSMOTIC CONCENTRATIONS OF EGGS

(7–8 days post-fertilization.)

Salinity ‰ (Δ)		Perivitelline fluid		Embryonic fluid	
Fertilization	Incubation	Δ	‰ NaCl	Δ	‰ NaCl
10·9 (0·65)	10·9 (0·65)	0·56	9·3	0·70	11·66
		0·57	9·5	0·68	11·33
32·3 (1·94)	10·9 (0·65)	0·64	10·7	0·68	11·33
		0·67	11·2	0·69	11·50
32·3 (1·94)	32·3 (1·94)	1·60	26·7	—	—
		1·67	27·8	—	—
32·3 (1·94)	47·8 (2·87)	2·07	34·5	0·90	15·0
		2·09	34·8	—	—
47·8 (2·87)	47·8 (2·87)	2·73	45·5	—	—
		2·69	44·8	—	—

TABLE 2. OSMOTIC CONCENTRATION OF EGGS AFTER TRANSFER

Salinity ‰ (Δ)		Time after transfer (h)	Perivitelline fluid		Embryonic fluid	
Incubation	Transfer		Δ	‰ NaCl	Δ	‰ NaCl
32·3 (1·94)	10·9 (0·65)	24	0·64	10·7	0·63	10·5
	32·3 (1·94)	24	1·67	27·8	—	—
	47·8 (2·87)	24	2·46	41·0	—	—
	10·9 (0·65)	48	0·61	10·2	—	—
	32·3 (1·94)	48	1·70	28·3	—	—
	47·8 (2·87)	48	2·70	45·0	—	—

The water content of the perivitelline fluid is higher in eggs incubated at the low salinities. This content, however, also depends on the salinity at fertilization. Very limited readings for the embryos suggest that their water content is also higher at the lower salinities.

Eggs were also transferred from sea water to a higher and a lower salinity before hatching, and freezing-point determinations made after 24 and 48 h. The results are shown in Table 2. The concentration of the perivitelline fluid seems to be greatly dependent on that of the environment but there does seem to be a slight measure of regulation. Unfortunately the samples from the embryos had nearly all to be discarded.

Time to hatching and percentage hatching. The time from fertilization to that when 50% of the larvae hatched was the same (11 days) for all salinities

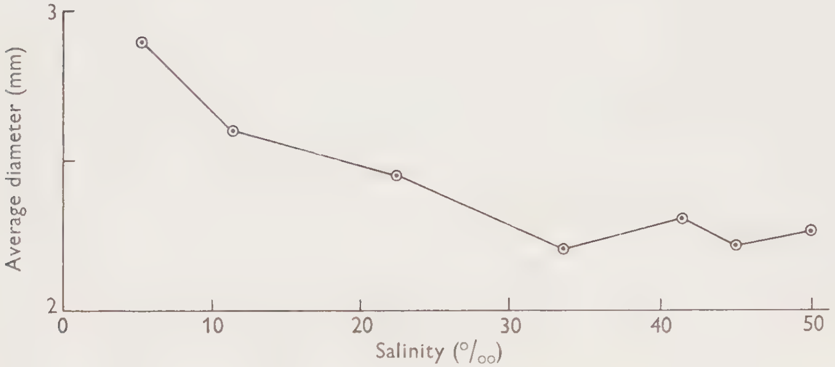

Fig. 2. Size of developing eggs.

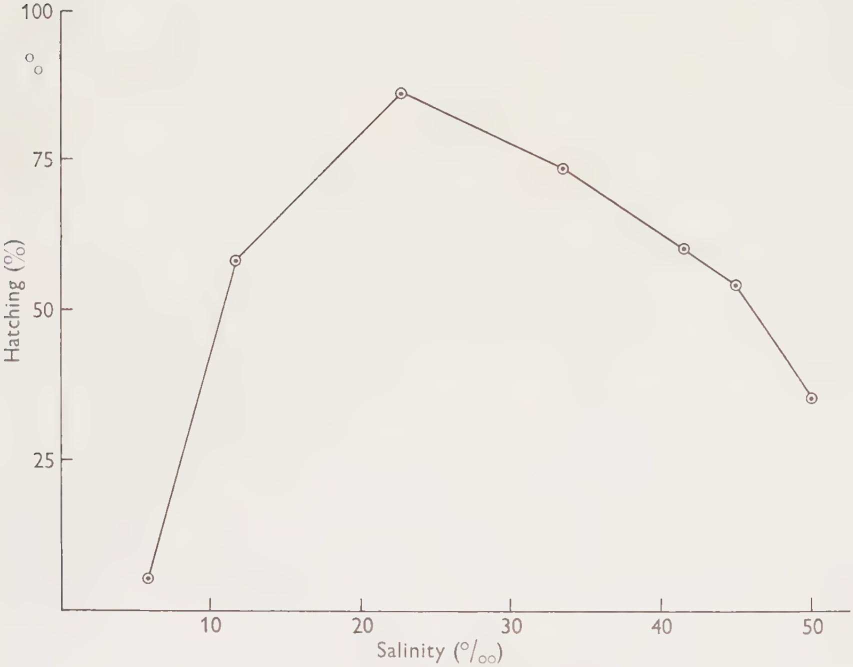

Fig. 3. Percentage hatching of eggs.

of incubation except 5·9 and 11·5‰, where the time to hatching was about 2 days longer.

The percentage hatching in different salinities is shown in Fig. 3. There appears to be an optimum range of salinity from about 20 to 35‰ and it appears that extremes of salinity impose more limitations on development.

LARVAE

Morphological characters. Observations were made on length, weight, appearance and activity of larvae on hatching. The results are shown in Table 3.

TABLE 3. LENGTH, WEIGHT AND APPEARANCE OF NEWLY HATCHED LARVAE

(Each value is the mean of ten larvae.)

Incubation salinity (‰)	Mean length (mm) (and S.E.)	Mean weight (mg)	Colour and shape of yolk sac
5·9	8·75 ± 0·037	0·90	Pale yellow; oval
11·5	7·85 ± 0·085	0·90	
22·7	7·90 ± 0·10	0·84	
33·6	6·43 ± 0·075	0·75	Dark yellow; spherical
41·6	6·70 ± 0·16	0·70	
45·0	6·90 ± 0·11	0·71	
52·5	6·75 ± 0·053	0·60	Intense yellow, shrunken and hard

The larvae hatched in salinities of 5·9, 11·5 and 22·7‰ were larger but the time to hatching tended to be longer in the lower salinities. There was, however, a negative correlation between weight and salinity. This was probably a reflexion of water content (see later description of freezing-point determinations) as larvae in high salinities would have a tendency to be dehydrated. This probably also explains the difference in appearance of the yolk sac and Ford's (1929) observations that a decrease in the specific gravity of larvae took place with reduced salinity of incubation.

Salinity tolerance. The range of salinities in which survival is possible is restricted to those in which the regulatory mechanisms of the animal can maintain the body fluids within certain limits. Outside this range, despite the functioning of the regulatory mechanisms, there is a continuous change of the body fluids from normal. The survival time will then depend, first, on the speed of the change, which will be greatest in the more extremes of salinity, and secondly, on the ability of the cells to function in conditions which are not optimum. Larvae were transferred in batches of ten from incubation salinities of 11·5, 20·5, 33·6 and 52·5‰ to 500 ml. jars holding a wide range of salinities from 0 to 70‰. The criteria of tolerance used were that 50% of the larvae should survive 24, 48 or 168 h immersion in the particular salinity. Thus the upper and lower limits of tolerance for 24 h may be considered as the high and low lethal salinities for herring larvae on the same basis used by Blaxter (1960) for temperature tolerance.

The results for these experiments are shown in Fig. 4. The most striking result is the extremely wide salinity tolerance, from 1·4 to 60‰, over 24 h to 2·5–52·5‰ over 168 h. A few larvae even survived in 60‰ for 168 h. At the end of the 24 h period some larvae were still alive (i.e. the heart was

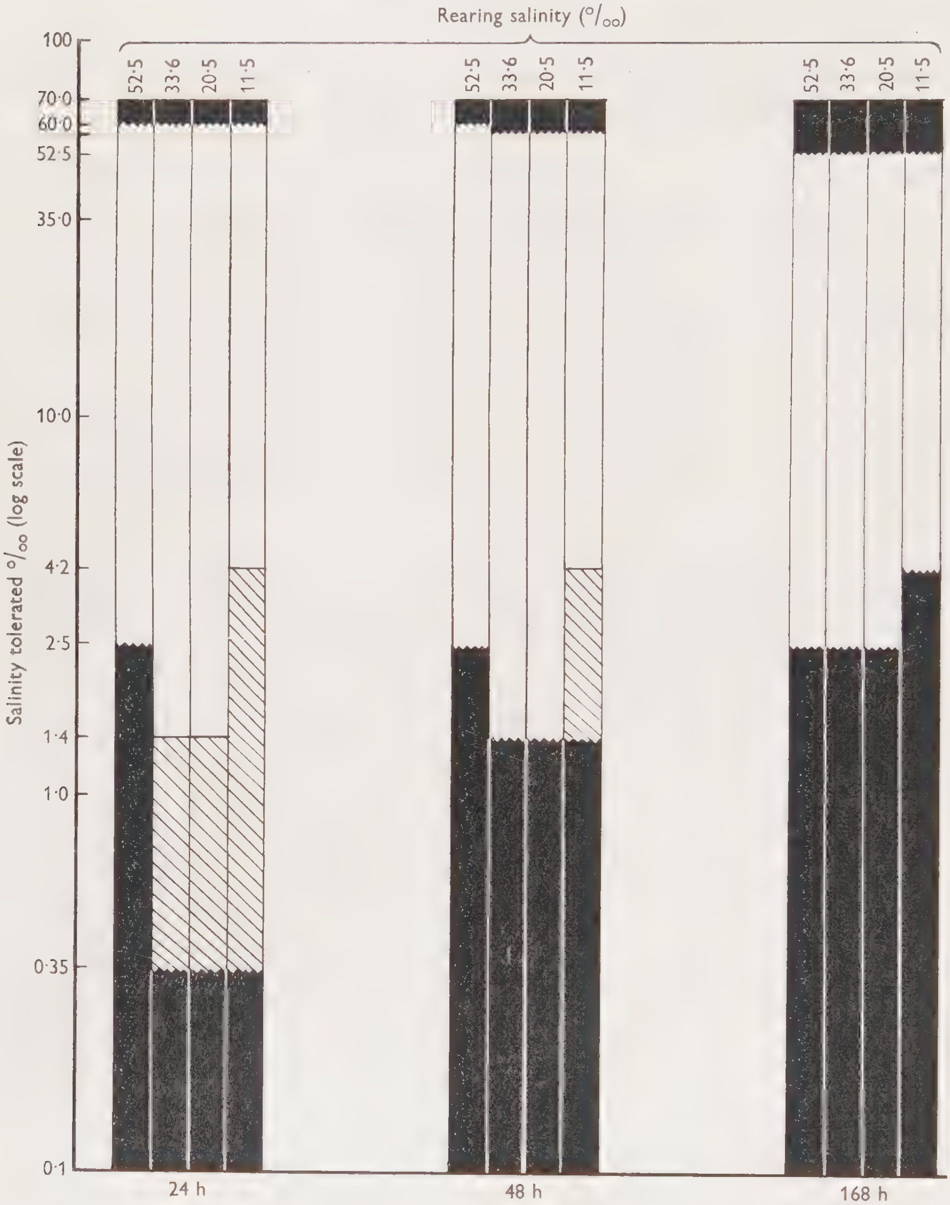

Fig. 4. Salinity tolerance of herring larvae. Shaded areas, < 50 % survival. Unshaded areas, > 50 % survival. Hatched areas, > 50 % survival, inactive but heart beating.

beating) but inactive, between salinities from 0·35 to 1·4‰. This is also shown in Fig. 4. There is a tendency for larvae incubated in the low salinities to have a greater tolerance of low salinities and larvae incubated in high salinities to have a greater tolerance of high salinities, but this is not consistent. There was very little tolerance of distilled water; the larvae either died or became inactive within 45 min. In this period of inactivity, which sometimes lasted for as long as 18 h before death, the rate of heart beat was reduced from a normal average rate of about 1·1 beats/second to an average of 0·7 beats/second. The body, and in particular the eyes swelled considerably before death. However, larvae recovered if they were transferred back to sea water within 18 h of being put in distilled water.

No difference was found between the salinity tolerance of spring- and autumn-spawned larvae.

Weight changes. It is well known (Summer, 1905; Black, 1948) that when fish are transferred from one salinity to another they undergo weight changes which correspond with movements of water into and out of the body.

Batches of fifty larvae were transferred from a salinity of 33·6‰ to salinities of 3·0, 11·4, 33·6 (control), 45·0 and 56·3‰. The weight of the larvae at the start of the experiment was measured by taking two samples of twenty larvae straight from 33·6‰. All weighings involved killing the larvae, and were done in a consistent manner. The larvae were removed from the water and placed on filter-paper to absorb excess water. For each sample identical methods of handling and exposure to the air were used. The change in weight in the different salinities is shown in Fig. 5, weighings being carried out after 6 and 24 h on samples of twenty larvae. There were changes in weight after 6 h consistent with water entering the body in salinities up to 11·4‰ and being lost in higher salinities. There is a tendency for loss of water at these higher salinities to be corrected after 24 h.

Osmotic concentrations. Freezing-point determinations (Δ) were made on larvae which had experienced different salinities to see whether these could be correlated with weight changes and salinity tolerance.

TABLE 4. OSMOTIC CONCENTRATIONS OF NEWLY HATCHED LARVAE

Incubation salinity ‰	(Δ)	No. of observations	Δ (and S.E.)	‰ NaCl
10·9	(0·65)	8	0·64 ± 0·002	10·7
32·3	(1·94)	10	0·74 ± 0·003	12·3
47·8	(2·87)	10	0·82 ± 0·012	13·7

First, the mean Δ's for ten larvae from each of three incubation salinities (10·9, 32·3 and 47·8‰) were measured. These are shown in Table 4. They show that the concentration of the internal body fluids does vary with the external salinity but in high salinities it is regulated and is well below the external salinity. The body-fluid concentration in sea water (here 32·3‰) is equivalent to 12·3‰ of salt. This may be taken as about the normal level for herring larvae in the sea.

Secondly, Δ's were determined on larvae which had been transferred from one salinity to another. Three series of experiments were carried out. In the first larvae were transferred from a salinity of 32·3‰ to a range of salinities from 3·3 to 60·1‰, body-fluid samples being taken after 3, 24 and 48 h. The results are shown in Fig. 6. In the second, larvae were transferred from 32·3‰ to distilled water, 3·3 and 60·1‰ and samples taken after 30 min, 1 h and 3 h. The results are shown in Fig. 7. Finally larvae from 11·2‰ were transferred to a range of salinities from 3·3 to 60·1‰ and samples of body fluids taken after 24 h (see Fig. 8).

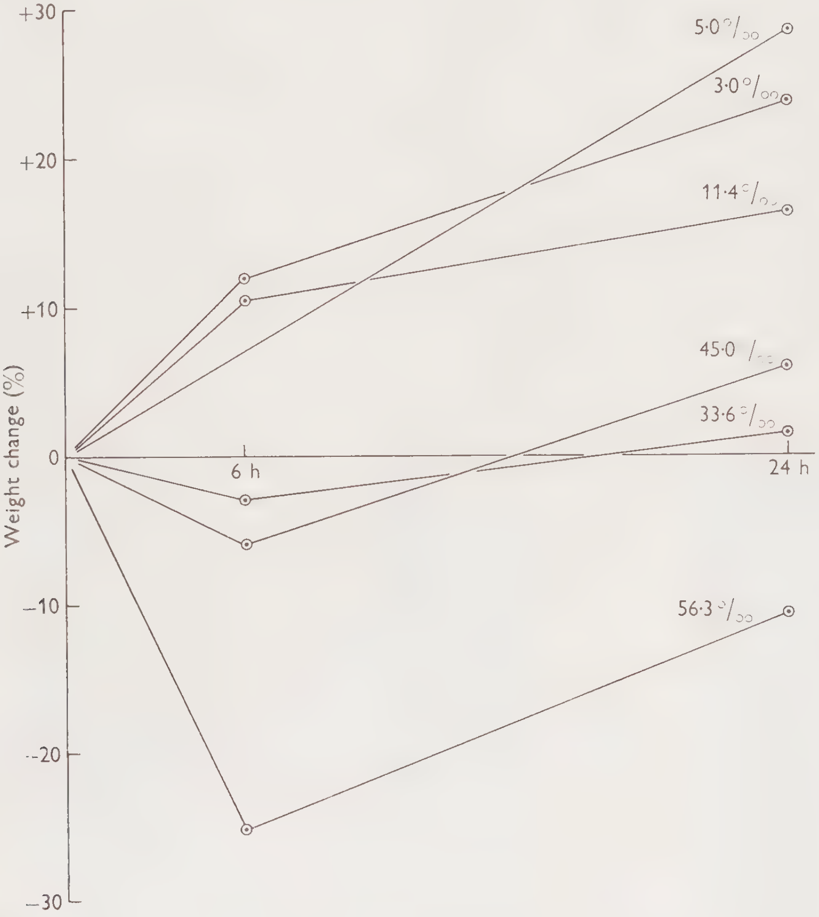

Fig. 5. Changes in weight of larvae when transferred from sea water to the given salinity.

The results show that there are considerable changes in the concentration of the body fluids when larvae are transferred, though regulation starts to take place within about 3 h. As samples were only taken from healthy larvae, the tissues of the body can presumably withstand these extremes of 'salinity' which may be as high as 27·5‰ and as low as 8·7‰ (the normal level being 12·3‰).

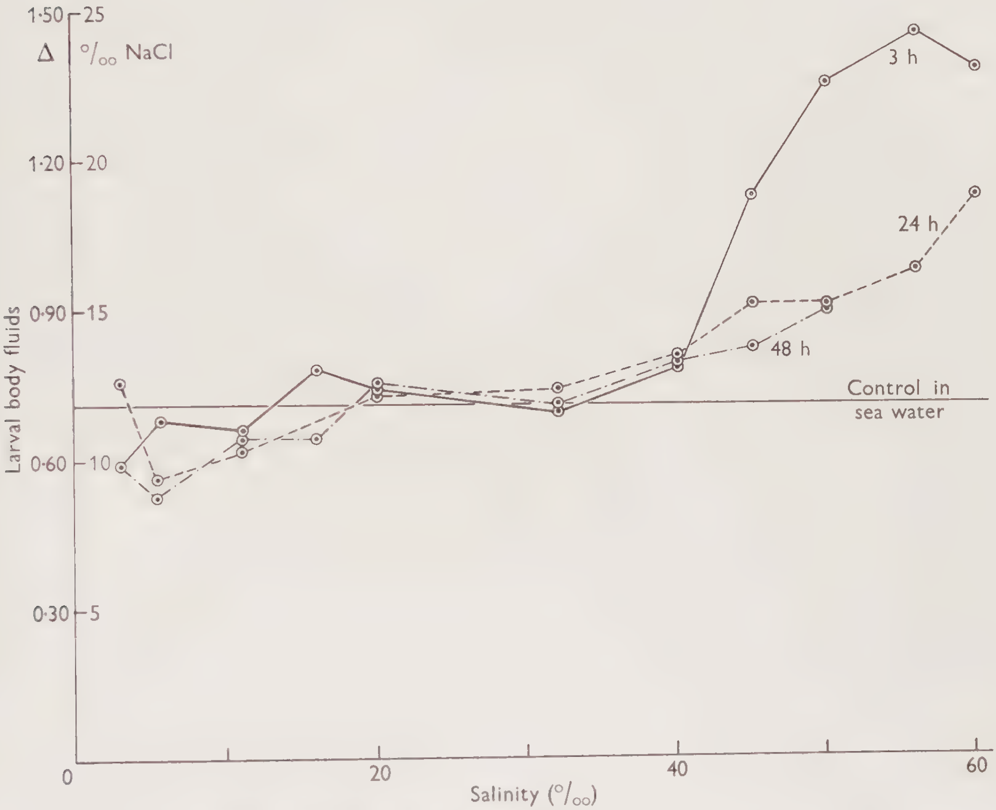

Fig. 6. Osmotic concentrations of larval body fluids. Larvae transferred from sea water (32·3‰).

The levels at which the body fluid concentrations become lethal seem to be equivalent to about 6 and 30‰ NaCl.

Sites and mechanisms of regulation. These are considered in adult fish to be the kidney and an extra-renal route for salt exchange, probably in the gill membranes. Very little is known about regulation in fish larvae.

Holstvoogd (1957) found a well-developed pronephric glomerulus and archinephric duct in herring larvae 10 mm long. Serial longitudinal and vertical sections were cut of larvae used in these experiments (up to 8·5 mm long). No sign of a kidney could be found, nor had the gills developed at this stage.

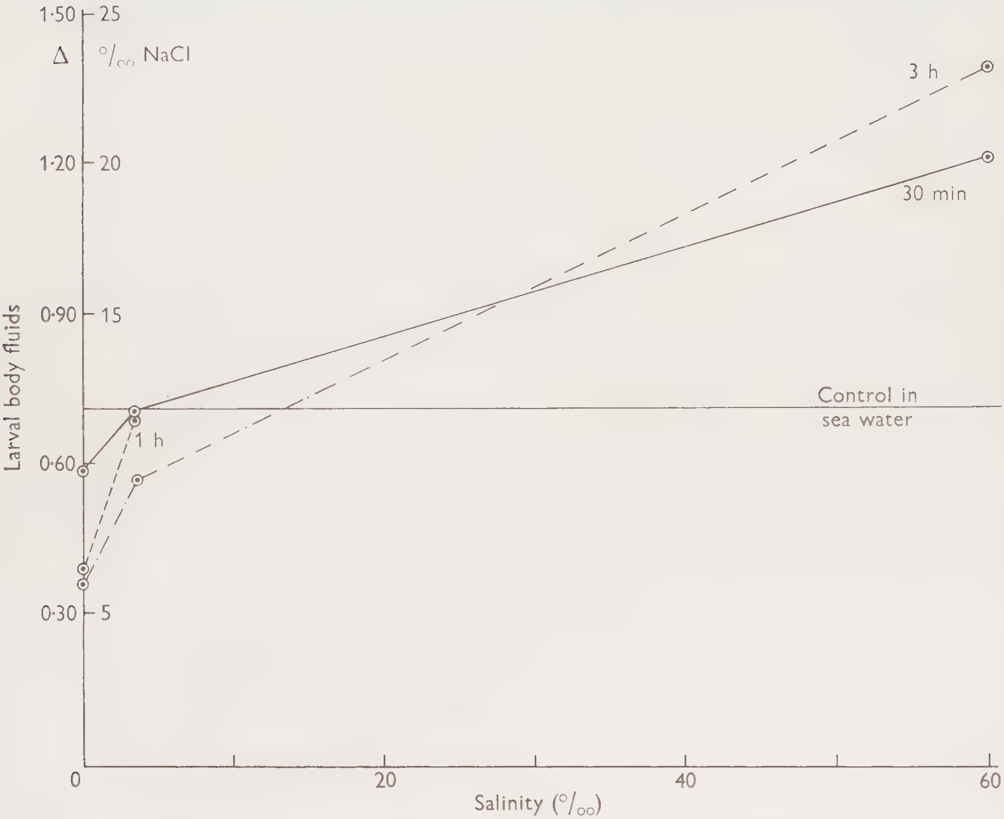

Fig. 7. Osmotic concentrations of larval body fluids. Larvae transferred from sea water (32·3 ‰).

DISCUSSION

The most striking results which came from this work are, first, that herring larvae can withstand external salinities ranging from 1·4 to 60·1 ‰ for 24 h and that they have a slightly reduced range of tolerance over longer periods. Secondly, the tissues themselves can withstand for a short time internal concentrations equivalent to salinities of about 9–28 ‰ though the normal value in sea water is 12 ‰. Thirdly, they have a mechanism for regulating the body-fluid concentration. Thus, when larvae are transferred to salinities within the range of 2·5–52·5 ‰, the body fluids are regulated to equivalent salinities 9·8–15·0 ‰. The salinity tolerance of newly hatched larvae is, in fact, wider than that of the adult (Holliday & Blaxter—unpublished to date), although the adult has well-developed sites for regulation. The wider salinity tolerance of the larvae, despite its lack of kidney and gill membranes, is probably due to the greater tolerance of the individual tissues as well as some presumed regulatory process.

The sites of this regulation have not yet been determined; Shelbourne (1957*a*) suggests the epidermis as a site for the regulation of salt in plaice larvae. The technique used to demonstrate this is not completely specific, however, so that the issue is not yet decided. Shanklin (1954) showed in *Fundulus* embryos that if the glycolytic pathways of metabolism were blocked by specific inhibitors, the embryos failed to osmoregulate, whereas they could normally survive in salinities from tap water to double strength sea water.

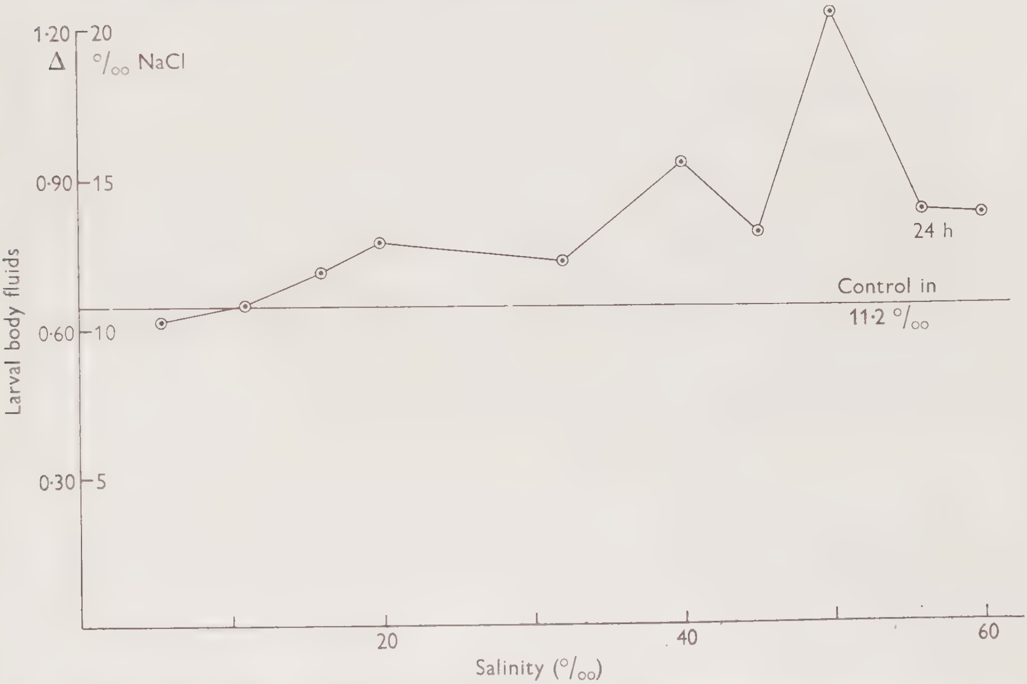

Fig. 8. Osmotic concentrations of larval body fluids. Larvae transferred from salinity 11·2 ‰.

The conclusion may be reached that herring larvae are relatively independent of salinity and that they are unlikely to be adversely affected by any salinity change which might take place in the sea or in rearing tanks. They are also more tolerant to salinity than the adult. This is in contrast to Shelbourne's (1957*b*) conclusions based on work with plaice. He considers that the osmotic hazard is one of the greatest dangers facing plaice larvae and that this danger decreases in the adult stage.

We should like to thank Dr G. Parry of the Ministry of Agriculture, Fisheries and Food Freshwater Fisheries Laboratory for much advice and help, and to Mr Parrish of this laboratory for his encouragement and advice.

SUMMARY

Fertilization, development and hatching of herring eggs occurred in salinities ranging from 5·9 to 52·5‰. Both the developing eggs and the larvae were larger when incubated in the lower salinities, and their relative water contents higher.

The salinity tolerance of both spring- and autumn-spawned larvae was found to lie between 1·4 and 60·1‰ for 24 h and between 2·5 and 52·5‰ for 168 h.

Determinations of changes in weight and body-fluid concentrations, when larvae were transferred from one salinity to another, demonstrated that extensive osmotic changes occurred in the body fluids. Under these conditions larvae experienced and survived internal body fluid concentrations equivalent to salinities of 8·7–27·5‰. A regulatory mechanism exists, however, which returns the body fluids within 24 h to a more limited range (around 12·3‰).

It seems unlikely that the osmotic forces met with in nature will constitute a serious hazard to the herring larva.

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THE EFFECT OF EXTREMES OF TEMPERATURE ON HERRING LARVAE

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(Text-fig. 1)

Most of the work on temperatures lethal to fish has been reviewed by Brett (1956). Most of the fish have been adults of freshwater species, and it has been found that both upper and lower lethal temperatures vary with the species, the temperature of acclimatization and the duration of time the fish are subjected to the test temperature.

Experiments on the upper and lower lethal temperatures for herring larvae (*Clupea harengus* L.) were started for three reasons: (1) to find out the range of temperature the larvae could withstand in rearing experiments at different acclimatization temperatures, this being part of a programme to determine the tolerance of herring larvae to a number of environmental factors (Holliday & Blaxter, 1960); (2) to look for possible differences in temperature tolerance between larvae from spring- and autumn-spawned herring (see Blaxter, 1958, for a discussion of this problem); and (3) to obtain some idea of what danger larvae might experience if subjected to rises of temperature in the sea caused by effluents or hot weather.

MATERIALS AND METHODS

Ripe gonads were dissected from spring-spawning herring caught in the Firth of Clyde in February 1957 and from autumn-spawning herring caught off the East Coast of Scotland in September 1957. The gonads were stored at 4° C (Blaxter, 1955) and transported to the laboratory, where the eggs were fertilized and hatched in tanks holding 50 l. of sea water (Blaxter, 1956). In February three tanks were used and maintained at different incubation temperatures (7·5, 11·0, 15·0° C). In September tanks at temperatures of 11 and 15·5° C only were used. These were also the acclimatization temperatures for the succeeding experiments.

Hatching occurred 7–15 days after fertilization, depending on the incubation temperature. The larvae were then 6–8 mm long and possessed yolk sacs. Within 2 days of hatching batches of ten larvae were transferred by a pipette from the incubation tanks to jars holding 500 ml. of sea water at the temperature of incubation. These jars were then placed in baths holding water at the test temperatures. The high-temperature baths, for testing the upper lethal temperatures, were maintained at their temperature by low-power immersion heaters controlled by thermostats. The low-temperature baths were either kept in a refrigerator or were cooled by glycerol from a refrigeration unit. The glycerol was circulated through a cooling coil by a small centrifugal pump controlled by a thermostat.

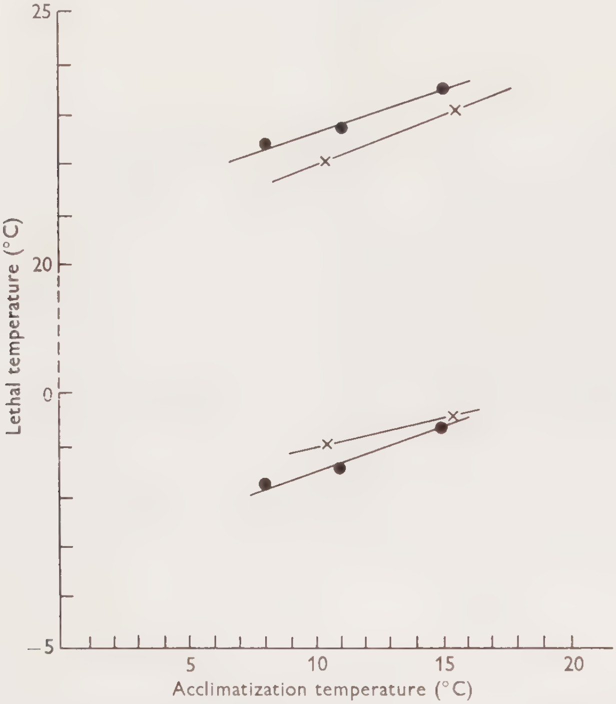

Fig. 1. Lethal temperatures for spring-spawned herring larvae (●—●) and autumn-spawned larvae (×—×) at different acclimatization temperatures.

The temperature of the water in the 500 ml. jars reached the test temperature within 1 h. Although continuous records were not kept, no observation of the test temperature showed a fluctuation greater than ±0·1° C during an experiment.

The numbers of larvae which were moribund or dead after 24 h at the test temperatures were counted. Larvae were called moribund when they had started to turn opaque though the heart continued to beat. Tests showed that this condition was not reversible. The scale of test temperatures (each one differing by about 0·5° C from the next) was such that at one end all the larvae survived and at the other at least 50% were moribund or dead.

RESULTS

The lethal temperatures, in this case defined as the temperature at which 50% of the larvae died or became moribund after a 24 h period of exposure, were determined in the following way. For each acclimatization temperature a graph was drawn of the percentage of larvae dead or moribund after 24 h at each test temperature. By interpolation the temperature at which 50% died or became moribund was determined. The lethal temperatures for both spring- and autumn-spawned larvae are plotted against the acclimatization temperature in Fig. 1. It will be seen that the range of lethal temperature is less for autumn- than for spring-spawned larvae. This difference was checked by probit analysis and found to be not significant.

DISCUSSION

The upper lethal temperatures (22–24° C) for herring larvae acclimatized to 7·5–15·5° C are very similar to those (22–25° C, over the same acclimatization range) for five species of salmonid fry studied by Brett (1952). The lower lethal temperatures for the herring larvae are, however, –0·75° C to –1·8° C, compared with 1–5° C for the salmonid species. Colton (1959) observed mortality at sea among the larvae of *Limanda ferruginea* and *Merluccius bilinearis* when they had probably been subjected to a rise in temperature from 6·7 to 17·8° C in 24 h. Kuthalingam (1959) found that the tolerance range for the larvae of ten species of tropical fish was very narrow, the upper lethal temperature varying from 30 to 31° C and the lower one from 27 to 29° C.

Although the test period of 24 h used in these experiments is an arbitrary one, it has been quite generally used in the past. Since the work of Doudoroff (1945) and Fry, Hart & Walker (1946) it has been more usual to determine the lethal temperatures by plotting the percentage dying at a given temperature against time. These authors found in nearly every test that all deaths occurred within the first 24 h at upper lethal temperatures. For lower lethal temperatures, deaths may continue to occur for up to 5 or 6 days depending on the test temperature. It has not been practicable to use this technique for herring larvae on hatching as they only survive this stage for about 1 week to 10 days and a sufficient number of experiments could not be carried out in this time. The upper lethal temperatures obtained in these experiments, then, may be compared with those determined by different criteria, but the lower lethal temperatures are probably rather lower than might be obtained by longer-term experiments.

Although the lethal temperature differences between spring- and autumn-spawned larvae are not significant, other physiological differences have been shown between larvae from spring- and autumn-spawning herring (Blaxter, 1956), and both Hart (1952) and McCauley (1958) have shown that lethal temperatures may vary in different races of the same species.

Thanks are due to my colleague Mr W. Hall for his help with the statistical treatment of the results.

SUMMARY

For herring larvae 6–8 mm long, acclimatized to temperatures between 7·5 and 15·5° C, the upper lethal temperature (defined as that temperature at which 50% of the fish die or become moribund after 24 h) varies from 22 to 24° C and the lower lethal temperature from −0·75 to −1·8° C.

The range of temperature tolerance is slightly less for autumn-spawned larvae than for spring-spawned larvae though this difference is not significant.

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DIRECT OBSERVATIONS ON SOME MANX SUBLITTORAL ALGAE

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(Text-figs. 1 and 2)

The recent spread of the free-diving technique has made direct contact with the sublittoral environment relatively simple. The advantages of this to the ecologist need not be stressed.

The rather more cumbersome and expensive standard diving method had had already been used by Gislén (1930), Kitching, Macan & Gilson (1934), Kitching (1937, 1941), Zalokar (1942), Bursa, Wojtusiak & Wojtusiak (1948) and Waern (1952). Drach (1948*a*, *b*, 1949, 1951) was the first to exploit free diving for ecological purposes and was followed by Forster (1954, 1955, 1958), Pérès & Piccard (1949), Ernst (1955), Laborel & Vacelet (1958), Knight-Jones & Clifford Jones (1956) and Aleem (1956).

Compared with the littoral region, the sublittoral of the British coast has been necessarily neglected. A certain amount of information has been collected by mechanical means (Chapman, 1947; Walker, 1947; Lodge, 1954), and where the bottom is smooth and the algae attached to small stones or unattached (Burrows, 1958) a grab can be as reliable as a diver. It is the detailed flora of the uneven rock surfaces which, with the exception of Kitching's admirable studies with a diving helmet, has defied description. Forster has included the more important plants in his studies, and Knight-Jones has made small collections.

It is clear that these studies are still in the descriptive stage. A certain amount of description of the flora must precede any attempt at distinguishing the factors. It is for this reason that the preliminary picture which has been obtained of the sublittoral algae of some parts of the south end of the Isle of Man is being presented here. This should be more than of local interest; it should give an indication of the type of vegetation which exists below low water on rocky coasts of Britain. A general qualitative description of the distribution of the more important algae with depth on the rocky parts of the coast was all that was attempted at first.

The nomenclature used is that given in the 'Preliminary Check List' (Parke, 1953) and the corrections to it (Parke, 1956, 1957). Where reliable taxonomic information was lacking, aggregates were used. Thus plants of *Nitophyllum* and *Polyneura* were grouped under *Nitophyllum* agg.; four-siphoned plants of *Polysiphonia*, other than *P. elongata*, were called *P. urceolata* agg. when ecorticate and *P. violacea* agg. when corticate.

METHODS

In order to cover as much ground as possible in this preliminary survey it was necessary to employ a sampling technique that was simple and rapid.

The depth was measured with a metre-long capillary tube gauge and expressed as metres below 'extreme low-water springs' (ELWS) by allowing for the height of the tide at the time of the dive. This was calculated in advance, using the data given by the *Admiralty Tide Tables* and Southward (1953), and corrected for deviation from the predicted height from observation of the Port Erin tide pole.

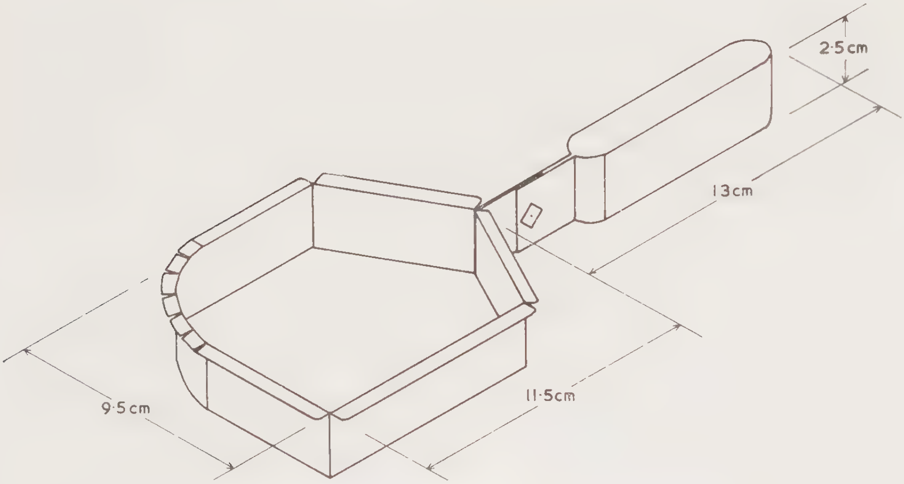

Fig. 1. Diagram of the scraper used, without the net bag.

The algae were removed from the rock with the aid of a scraper (Fig. 1), shaped somewhat like a miniature dredge. This was made from strip iron, had the lower leading edges sharpened, and bore a flange around the upper edges. A bag made from mosquito netting and measuring 40 cm in circumference and 66 cm in length had its neck drawn in by elastic cord. This fitted over the flange on the scraper and could easily be removed and replaced under water. The net had a wooden clothes peg attached near the neck and a roughened plastic label. The sharpened edge of the scraper easily removed the bases of most algae, except encrusting calcareous forms and large laminarians. The thalli so released passed into the net bag and were held there by the water passing through as the instrument was moved.

A rapid survey of a chosen place was made by collecting samples of the flora from several rock faces at intervals of approximately 1 m of depth from ELWS to the lowest level of the rock itself. The net bag on the scraper was changed between each sample, the depth and substratum noted on the label and the bag attached by means of the clothes peg to a carrier. Each sample was examined in the laboratory and the species listed with notes on reproductive structures and a subjective abundance score. An exhaustive search for species was not made. *Lithothamnion* and related genera were ignored.

To show how far results were repeatable six levels at Port Erin breakwater were sampled twice within a few days. The general picture given of the distribution of the main species was similar in the two surveys, but the danger of attaching too much importance to the abundance scoring was emphasized by the apparent commonness of one species (*Delesseria sanguinea*) in one survey and its rarity in the other. Most of the places were sampled at one season of the year only, but Port Erin breakwater was sampled at regular intervals for one year for an indication of seasonal changes.

THE REGION

The places sampled all lie off the south-west end of the Isle of Man between Niarbyl and Langness (Fig. 2). This part of the coast is mainly rocky, with sand or shingle in the bays of Fleshwick, Port Erin, Perwick, Port St Mary, and Castletown. The sublittoral flora of these bays, where the bottom is relatively flat, forms a study in itself (Burrows, 1958) and has not been included here. Along much of the rest of the coast there are cliffs, varying in height and steepness. Below these sublittorally there are usually boulders, varying in size and extent with the topography of the cliffs. Opposite gullies the boulders have accumulated; below sheer cliffs they are fewer and more steeply stacked. In no place so far visited, however, do vertical cliffs extend for more than a few metres below ELWS; the slope of the rock is always more gentle. In certain places there are outcrops of solid rock either amongst the boulders or offshore from them. These form reefs of various shapes. The rocky bottom, whether formed of solid rock or boulders, always gives way at a depth of 8–21 m (mainly at about 12 m) below ELWS to an unstable bottom of gravel or sand. Where the boulder bed slopes gently this change is gradual, there being gravel between the boulders for some distance before the gravel bed itself.

The principal factors likely to be important in the sublittoral environment will be briefly reviewed. They are, of course, interrelated.

The temperature of the sea varies between about 6 and 15 C (Slinn, 1959). Except occasionally in the sheltered bays, and on rare occasions offshore in unusual weather conditions, there is little temperature stratification in this region. Taken by itself, therefore, temperature cannot be a factor determining the position of sublittoral species. The same applies to the concentrations of the major nutrients.

The substratum, on the other hand, is an extremely important factor in determining the algal distribution. As has been seen, the extent of rock surface suitable for colonization is very limited; much of the bottom is occupied by gravel. This latter may on occasion provide a suitable substratum for certain forms, but it seems likely that for much of the year not only is it uninhabitable itself, but its presence may reduce the suitability of some parts of the rock surfaces. The general topography of the rocks is important, the slope and aspect clearly affect the light intensity received, and may also have a bearing on the possible effect of the settling or scouring by sand or gravel. The type of surface does not vary a great deal and does not seem greatly to affect colonization.

It is likely that water movements affect algal distribution in a variety of ways. The tidal streams are in some places fairly strong, reaching 5 knots at springs in the vicinity of Calf Sound, and in other places are negligible. They may have some effect on the distribution of spores, and where they are strong growth may be affected through the provision of nutrient. The turbidity of the water and thus the light penetration is slightly increased at spring tides, but there is not the marked variation in underwater visibility that is so noticeable on other coasts.

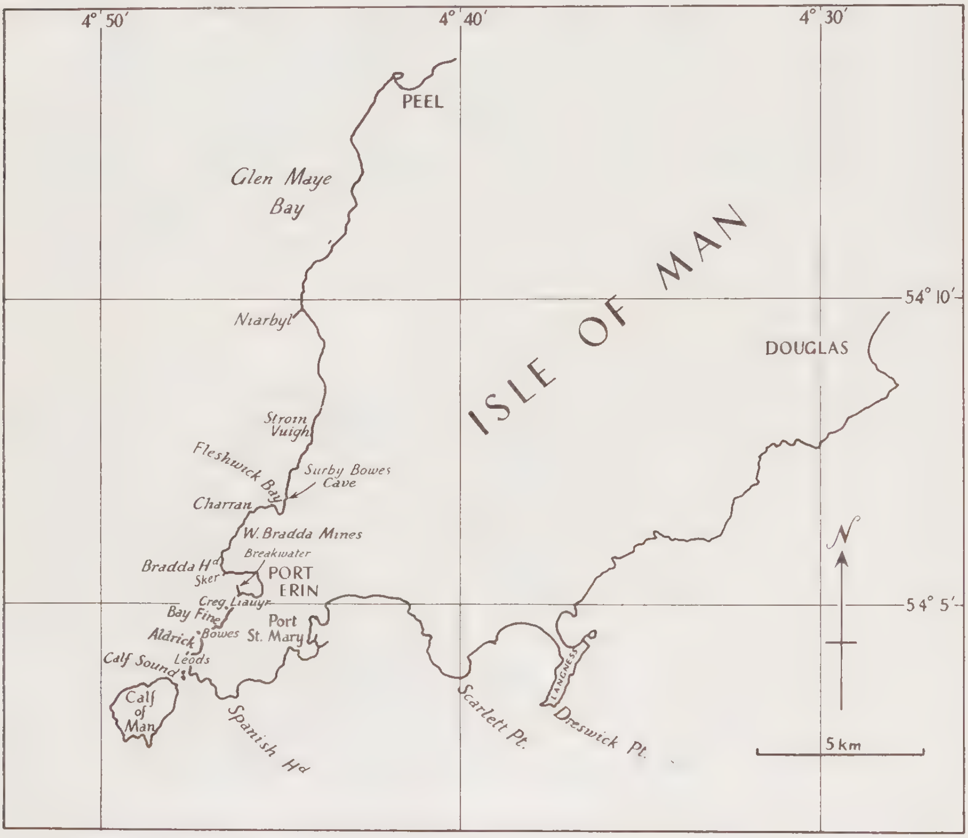
4° 50′
4° 40′
4° 30′
PEEL
Glen Maye Bay
ISLE OF MAN
54° 10′
Niarbyl
DOUGLAS
Strom Vuigh
Fleshwick Bay
Surby Bowes Cave
Charran
W. Bradda Mines
Breakwater
Bradda Hd
Sker
PORT ERIN
Creg Liauyr
54° 5′
Bay Fine
Aldrick
Bowes
Port St. Mary
Calf Sound
Leods
Calf of Man
Spanish Hd
Scarlett Pt.
LANGNESS
Dreswick Pt.
N
5 km

Fig. 2. Outline map of the south end of the Isle of Man.

Water movement of what is probably a more important type is caused by wave action. This is a notoriously difficult factor to measure on the shore and it is not any easier sublittorally. Its importance for a considerable depth below ELWS is beyond doubt during gales, as large quantities of sublittoral vegetation are washed on shore. It is possible that under more extreme conditions the water motion and the movement of solid material could be very considerable in the depth range under consideration. The movement of solid material could have indirect effects both on water turbidity and thus light penetration, and possibly through scouring action or settling on rock surfaces. The effects of gales on turbidity is just noticeable subjectively, but is not marked because there is no reservoir of suspendable material in the form of shallow water mud beds.

Light is clearly an important factor affecting algal distribution with depth. Direct measurements in these waters have only just begun and cannot yet be presented. It must now suffice to say that compared with many British waters the transmission is high and the compensation point for many algae subsequently deep. During the day there is sufficient light to see clearly at 35 m in summer, though of course it is virtually monochromatic.

ROCKY BOTTOMS

The places that have been studied will be described in turn around the coast. The records for all the species are given in Tables 1–3.

Niarbyl

At Niarbyl there is a conspicuous reef extending south-westwards from the shore, much of it above high-water level. The sublittoral part of the reef extends farther south-westwards and is highly dissected, there being a number of knolls with nearly vertical sides, about 8 m high, set on a smooth rock plateau at about 10 m below ELWS. This plateau extends farther south-westwards for at least 100 m, gently sloping and reaching a depth of 16 m. On the lower parts gravel lies in slight fissures, and most of the surface is occupied by an ophiuroid bed. The point is subjected to fairly strong tidal streams.

The algae were sampled in May 1958 (Table 1). The vertical and upward-facing slopes of the rocky knolls were occupied by typical laminarian forest, with *Laminaria hyperborea* dominant. An undergrowth to this was formed by *Dictyota dichotoma* (particularly abundant here), *Desmarestia aculeata*, *Cryptopleura ramosa*, *Delesseria sanguinea*, *Cutleria multifida* sporophyte and other species in smaller quantities. No *Callophyllis laciniata* was found here, though it was abundant in the forest farther south. *Alaria esculenta* occurred in places near the tops. The overhanging faces of the knolls bore few algae and were mainly occupied by the coelenterate *Alcyonium*. The zone of *Laminaria* had its lower limit at about 6–7 m below ELWS, leaving a gap of at least 2 m above the horizontal rock plateau. Most of the other common algae extended down through this region and also occupied much of the plateau. *Saccorhiza polyschides*, common in the lower parts of the *Laminaria* zone, tended to dominate just below it, both on the vertical rock faces and on the shallowest parts of the plateau at about 10 m. *Dictyota* was also abundant in these lower parts, together with large bushes of *Desmarestia*. The vegetation gradually thinned out along the lower slopes of the plateau and was very sparse at the outer end of the reef.

Stroin Vuigh

A ridge of boulders runs out from the shore between Niarbyl Bay and Fleshwick Bay. The solid rock of the shore itself extends to about 7 m below ELWS, with occasional knolls. The boulders are numerous at this level but thin out gradually farther offshore, until they are only occasional at 10 m, imbedded in fairly fine gravel. There is little or no tidal stream along this part of the coast.

The algae were sampled in July 1959 (Table 1). The usual *Laminaria hyperborea*

TABLE 1. THE SPECIES OCCURRING IN SAMPLES FROM ROCKY PLACES BETWEEN NIARBYL AND BAY FINE, AT VARIOUS DEPTHS

(+ = present; T – tetrasporangia; C = cystocarps; B = both tetrasporangia and cystocarps; P – plurilocular sporangia; p = propagules.)

	Niarbyl May 1958										Stroin Vuigh, July 1959			Surby Bowes Cave, Oct. 1959		Sker, May 1959			Creg Liauyr (N), Apr. 1958											Creg Liauyr (S), Apr. 1958											
Depth (m below ELWS)	1	2	3	4	5	6	7	9	11	13	5	6	7	0	1	6	9	11	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12
Chaetomorpha melagonium	+	–	+	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–			–	–	–	–
Ulva lactuca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–			–	–	–	–	–	–
Alaria esculenta	+			+							–											–	–			–			–	+	+	–	–	–		–	–	–	–	–	–
*Chorda tomentosa**		+		+	+	–				–							–		–		–	–	–								–	–	–		–	–	+	–	–	–	–
Cutleria multifida sporoph.	–	+	+	+	–	–		+	+	–			+			?	?	?	+	+	+	+	+	+	–	+	+	+	+		+	–	+	+	+	+	+	+	+	+	+
Desmarestia aculeata	–	+	–	+	–	–		+	+	–			+			+	+	+	–	–		–	+	+	+	–	+		–		+		+	–	+	+	+	–	+	–	–
D. ligulata	–															+	–		–	–	+	–			–	–				–		–	–		–	–	–	–	–	–	–
Dictyota dichotoma	–	+	+	+	+	+	+	+	+	+	+	+	T	–	–	+	+		+	+		+	+	+	–	+	–				–	–	–	+	+	–	+	–	–		–
*Ectocarpus confervoides**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+		–	–	–
*Giffordia hincksiae**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Halidrys siliquosa	–	–	–	–	+	–	–	+	+	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+		–	–	–	–	–		–
Laminaria hyperborea	+	+	+	+	+	–	–	–	–	–	+	+	–	–	–	+	–	–	+	+	+	+	+	+	–	–	–	–	–	+	+	+	+	+	+		–	–	–	–	–
L. saccharina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+			–	–			–	–	–	–	–
Pylaiella littoralis								–															–							+		–	–	–	–		–	–	–	–	–
Saccorhiza polyschides	–	+	+	+	+	+	+	+	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–	–	+	–				+		–	–	+	+	+	+	–	–	–	–
Sphacelaria pennata†	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+								–	–	–	–		–	–	–	–
S. plumula†	–	–	–	–	–	–	–	p	p	–	–								–	–						–							–		–	p	–	–	–	–	–
Spongonema tomentosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Apoglossum ruscifolium	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	–	–	–	–	–	–	–
Bonnemaisonia asparagoides	–	–	–	–	+	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
B. hamifera sporoph.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+		–	–			–	–	–		–	+	–	–	+	+	+
Brongniartella byssoides	–	+	–	–	+	+	+	+	+	+	T	–	T	–	–	+	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
Callithamnion hookeri	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
Callophyllis laciniata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	+	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Ceramium rubrum agg.	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	+	+	–	C	–	+

	Niarbyl										Stroin Vuigh			Surby Bowes Cave		Sker			Creg Liauyr (N)											Creg Liauyr (S)											
	1	2	3	4	5	6	7	9	11	13	5	6	7	0	1	6	9	11	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12
Chondrus crispus		–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Chylocladia verticillata	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cruoria pellita	–	–	–	–	–	–	–	–	–	–	–	–	–	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			–	–	–
Cryptopleura ramosa	+	+	+	T	+	–	–	+	+	+	T	T	B	+	T	+	+	+	+	+	+	+	+	+	+	–	–	+	–	+	+	+	+	+	+	+	–	+	–	–	–
Cystoclonium purpureum	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Delesseria sanguinea	–	+	+	+	+	+	+	+	–	+	+	+	–	–	–	–	+	+	+	+	+	+	+	+	+	+	–	–	+	–	+	+	+	+	+	+	+	+	–	–	–
Griffithsia flosculosa		–	–				–															–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–			–	–
Halarachnion ligulatum	–	–	–	+										–							–				–					–					–	–	–	–		–	–
Heterosiphonia plumosa	–	–	+	–	+	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hypoglossum woodwardii	–	–	–	–	+	+	+	+	+	–	–	–	T	–	–	–	–	–	–	+	–	–	+	–	+	–	–	–	–	–	–	+	+	–	+	+	+	+	–		–
Lomentaria clavellosa	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
L. orcadensis	–	–	–	–	–	T	+	–	–	–	–	–	–	–	–	–	–	–	–	T	–	T	–	–	–	–	–	–	–	–	–	+	T	–	–	–	–	–	–		–
Membranoptera alata	+	+	+	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	+	+	+	C	+	C	–	–	+	–	–	–	+	+	+	+	+	–	+	+	+		–
Nitophyllum agg.	–	–	–	–	+	+	+	+	+	–	–	T	C	–	T	–	C	+	–	–	+	+	+	+	+	–	–	–	–	–	–	–	+	–	–	T	–	–	+		–
Odonthalia dentata	–	+	C	–	–	–	+	+	+	–	–	+	+	–	+	–	+	–	+	C	C	+	+	–	–	–	–	–	–	+	+	+	+	+	+	+	–		–	–	–
Phycodrys rubens	+	+	+	+	+	–	+	+	+	–	+	+	–	–	+	–	+	–	+	+	T	B	+	T	+	+	+	+	–	+	+	+	+	T	+	–	T	C	+	–	–
Phyllophora rubens	+	+	–	–	–	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–
Plocamium coccineum	+	+	+	–	+	–	+	+	+	+	+	+	+	+	–	–	–	–	+	+	+	+	–	+	–	–	–	–	–	–	+	–	+	–	+	–	–	–	–	–	–
Polysiphonia elongata	–	–	–	–	–	C	+	C	+	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	T	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
P. urecolata agg.	–	–	–	+	–	–	T	+	+	+	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	–	+	–	–	+	–	–	+	–	–	–	+	–	–	–	–
P. violacea agg.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	B	T	–	–	–	–	–	–	–	–	–	B	–	–	T	B	–	–
Porphyropsis coccinea	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
Pterosiphonia parasitica	–	+	–	+	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+	+	+	+	–	+	+	+	+	–	–
Ptilota plumosa	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Ptilothamnion pluma	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhodomela confervoides	S	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Rhodophyllis divaricata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–	–	–	–	–
Rhodymenia palmata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	+	–	–	–	–	–	–	–	–	–	–
Spermothamnion sp.	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

* *Sensu* Hamel, 1931–9.
† *Sensu* Irvine, 1956.

TABLE 2. THE SPECIES OCCURRING IN SAMPLES FROM ROCKY PLACES BETWEEN BAY FINE AND LANGNESS, AT VARIOUS DEPTHS

(+ = present; T = tetrasporangia; C – cystocarps; O = oogonia; S = spermatangia; B = both tetrasporangia and cystocarps or oogonia; P = plurilocular sporangia.)

	Bowes Apr. 1958											Leods, July 1959		Spanish Head,														Scarlett, July 1959					Langness, July 1959				
														July 1959										Feb. 1960													
Depth (m. below ELWS)	5	6	7	8	9	10	11	12	13	14	15	2	14	3	6	8	10	13	15	17	18	20	22	13	16	19	22	2	3	5	7	8	4	6	8	11	12
Bryopsis plumosa	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ulva lactuca	—	—			—	—	—	—	—	+	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chorda tomentosa	—	—	—	—	+	—	—	—			—	—	—	—	—	—			—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cutleria multifida sporoph.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+	+	—	—	—	—	—
Desmarestia aculeata	—	+	+	+	+	+	+	+	+	+	+	+	—	—	+	+	+	+	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
D. ligulata	—	—	—	—		—			—	—	—	—		+	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dictyota dichotoma	+	+	+	+	+	+	+	+	+	+	+	+	+	+	O	+	O	+	B	+	+		—	—	—	—	—	—	—		+	—	—	—	—	—	—
Dictyopteris membranacea	—	—	—	—	—	—		—	—	—	—	—	+		—		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ectocarpus confervoides	—	—	—	—	—	—	P		—	—	—	—			—		—	—	—		—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—
*E. drapernaldioides**	—	—	—	—	—	—	—	—	—	—				P		P	—	—	—	—	—	—			—	—	—	—		—	—	—	—	—	—	—	—
*Giffordia granulosa**	—	—	—	—	—	+			—	—				—	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halidrys siliquosa	—	—	—	—	+	—				+	—						—	—	—	—	—							—	—	+	—	—	—	—	—	—	—
Laminaria hyperborea	+	+	+	+	+	+	—	—	—	—	—	+		+	+	+	+	+	—			—		+			—	+	+	+	+	+	+	+	+	—	+
L. saccharina	—	+	+	—	—	+	+		+		—		—			—	+	—	—	+	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—
Saccorhiza polyschides	—		—	—	+	—	+	+	+		—	—	—	+	—	+	+	+	+	+	+	—	—	+	+		—	—	—	+	+	—		—	—	—	—
Sphacelaria caespitula†	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—			—		—	P		—	—	—	—	—	—	—	—	—	—	—	—
S. plumula	—		—	—	—		—			+		—	—	—	—	—		—		—	—			—			—	—	—				—		—	—	—
Stictyosiphon tortilis‡	—	—	—	—	—			—		—					—	—		—		—	—	—				—	—	—	—	—	—	—	—	—	—	+	—
Antithamnion plumula	—	—	—	—	—	—	—	—	—	—				—	—	—		—	—	—	T	+	T	—	—	+	—	—	—	—	—	—	—	—	T	—	—
Apoglossum ruscifolium	—	—	+	+	—	—	—	—		—					C	B	—	—		—	C	—	—	—				—	C	—	+	—	—	—	C	—	T
Bonnemaisonia asparagoides	+	—	+	—	+	+	+	+	+				C		C	C	C	C	C	C	C	C	—	—			—	—	—			—	—	—	—	—	—
B. hamifera sporoph.			+	+	+	+	+	+	+	—	+	—	+	—	+	+	+	+	+	+	+	+	+		+	+	+	—	—	—	—	—	—	—	—	—	—
Brongniartella byssoides	—	+	+	—	+	+	+	+	+	—	+	—	—	—	—		+	—	+		—	—	—	—	—	—		—	—	—	—	—	—	T	—	—	—
Callithamnion tetragonum	—						—			—				+	+	C	+								—	—			—	+	—	—	—	—	—	—	—
Callophyllis laciniata	+	+	+	+	+	+	+	—	+		—	+	—	—	+	+	+	+	+	+	—	—	+	—	+	+		+	—	+	+	—	+	+	+	+	+
Ceramium rubrum agg.	—	—	—	—	—	—		—		—	—				—		—			—	—	—	—	—		—	—	—	—	+	—	—	—	—	—	—	—
Chondrus crispus	—	—				—						—	—	—					—					—	—	—	—			—	—	—	—	—	—	—	+
Composothamnion thuyoides							—	—					+	—	—	—		—	—	+	T	T	T	—				—	—	—		—	—	—	+	—	+

	Bowes											Leeds		Spanish Head														Scarlett					Langness				
														July 1959										Feb. 1960													
	5	6	7	8	9	10	11	12	13	14	15	2	14	3	6	8	10	13	15	17	18	20	22	13	16	19	22	2	3	5	7	8	4	6	8	11	12
Corallina officinalis	—	—	—	—	—							—												—	—			—	—	—	—	—	—	—	+	—	+
Cruoria pellita	—		—	—											—		—		—	—	—	—			—	—	—	T	+	+	+	+	—	—		—	—
Cruoriopsis gracilis	—	—										—					—		—	—		—			T		—				—	—		—		—	—
Cryptopleura ramosa	+	+	+	+	+	+	+	+	+	+	+	T		T	T	T	B	T	+	C	B	C		+				+	T	T	B	T	T	T	—	—	C
Delesseria sanguinea	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	+	—	—	—	+	+	—	—	+	T	—	—	+	+	+		+	+	—	+	—
Dilsea carnosa	—	—	—									—																+		+			+	—	+	—	—
Griffithsia flosculosa	—	—	—	—	—		—			—					—					+			—			+	—		+	—	+			+	—	+	+
Halarachnion ligulatum	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	C	—	C	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halymenia latifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	C	—	—	—	—	—	—	—												—	—
Heterosiphonia plumosa	—	+	—	+	—	—	—	+	—	—	+	—	—	—	—	—	—	—	—	+	+	—	—	—	+	+	+			+	+	+	+	+	+	+	—
Hypoglossum woodwardii	—	+	—	+	+	—	+	+	—	—	—	—	—	—	—	—	—	+	B	BS	+	—		+	+	C	—	—	—		—		—	T	C	+	C
Lomentaria clavellosa	—	—						—						—									—	—	—	T	—	—	—	—		—	—	—	—	—	—
L. orcadensis	+	+	—	+	T	T	+	T	—	—	T	—	—	—	—	—	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—		—		—
Membranoptera alata	+	+	+	+	+	+	—	—	—	—	—	—	—	+	—	+	—	—	—	+	—	—	—	—	—	—	—	+	—	—	+	+	—	—	+	—	+
Naccaria wiggii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nitophyllum agg.	—	—	—	—	+	—	+	—	—	—	—	—	—	—	—	B	B	T	C	B	T		+				+		C		T		—	—	+	+	—
Odonthalia dentata	+	—	—	—	—	+	+	—	—	—	—	+	—	—	+	+	+	—	—	—		—		—	—	—		+	+	+	—	—	+	+	+		+
Phycodrys rubens	+	+	+	T	+	+	—	—	+	+	+	—	+	+	+	+	+	+	+	+	+		+	+	—	+	—	+	+	+	+	+	+	+	+	+	—
Phyllophora membranifolia		—		—	—	—							—	—	—	—					—	—	—	—	—	—		—					—		—	—	+
P. rubens	+	—	—	—	—	—	+	+	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—		—	—	+	—	—	—	—
Plocamium coccineum	+	+	+	+	+	+	+	+	+			+	—	+	+	+	+	+	+	C	—	—			+	+	—	—	—	+	+	—	+	+	+	+	—
Polysiphonia elongata	—	—	—	—	—	—	—	—	—	—	—	—	—	—			—	—	+		—				—	—	—	—			—	—	—	—	—		—
P. urceolata agg.	+	+	—	+	+	+	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—		—		B
P. violacea agg.	—	—	—	—	—	—	—	—	—	—	—	—	—	T	+	T	T	+	—	—	—	—	—	+	—	—	—	—	—	C	—	—	—	—	—	—	—
Porphyra umbilicalis f. *rosea*	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	—	—	—	—	—	—		—	—	—	—	—		—	—			—	—	—	—
Porphyropsis coccinea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+		—	—	—		—	—		—	—	—	—	—	—
Pterosiphonia parasitica	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	C	+	+	C	C	C	+	+	+	+	+	+	+	+	+	+	+	+	—	+	—	+
Ptilota plumosa	+	—	+	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	+
Rhodomela confervoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—				—	—	—	—
Rhodochorton rothii (Turt.) Näg.	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhodophyllis divaricata	—	—	—	—	+	—	—	+	—	—	+	—	—	+	—	—	—	—	—	C	—	—	—	—	—	+	—	—	—	—	—	—	—	C	T	+	T
Rhodymenia palmata	—		—	—	—		—	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	—	—	—	—	—	+	—	+	—	+	+	+	—	—	—

* *Sensu* Hamel † *sensu* Irvine ‡ *sensu* Naylor, 1958.

TABLE 3. THE SPECIES OCCURRING IN SAMPLES FROM PORT ERIN BREAKWATER AT DIFFERENT SEASONS, AT VARIOUS DEPTHS

(+ present; T tetrasporangia; C cystocarps; O oogonia; S spermatangia; B both tetrasporangia and cystocarps; P = plurilocular and U = unilocular sporangia; p – propagules.)

	Mar./Apr. 1958								July 1958								Oct. 1958								Jan. 1959								Apr. 1959							
Depth (m. below ELWS)	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Bryopsis plumosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	+	+	+	—
Chaetomorpha melagonium		—		—		—	—	—	—	—	—	+	—	—	—		+	—					—	—		—	—		—	—	—	—	—	—	—	—	—		—	—
Ulva lactuca		+	—	—		—		—	+			+	+		—			—	—		+	+	—	+			—	—		—	—		+	—	—	—	—	—	—	+
Cutleria multifida sporoph.	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	U	+	—	—	—	+	+	+	+	+
Desmarestia aculeata	—	—	—	+	+	+	+	+	—	—	+	+	+	+	—	+	—	—		—	+	+	+	+			+	—	+	+	+	+	+	+	—	—	+	+	—	—
D. ligulata	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+	—
Dictyota dichotoma	+	+	+	+	+	+	—	—	+	T	+	T	T	T	+	—	+	—	O	+	T	+	+	O	—	—	—	—	—	—	—	—	+	—	—	+	+	+	—	+
Ectocarpus confervoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—		—	—	+	—	—	—	—	—	—	—	—	—	—	—
Giffordia hincksiae	—	—	—	—	—	—	—	—	—	—	—	—	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	P	—	—	—	—
Laminaria hyperborea	+	+	+	+	+	—	—		+	+	+	+				—	+	+	+	+	+	—	—		+	+	+	+	+			—	+	+	+	+	—	—	—	—
L. saccharina	—	—			—	—	—	—	—		—		—	—	—	—	—	—	—	—	+	—	—	+			—	—	+	—	—	+	+	—	—	—	—	—	—	—
Saccorhiza polyschides	—	—	—	+	+	+	—	—	+	+	+	+	+	+	—	—	—	—	+	+	+	+	—	—		+	—	+	+				+	+	—	+	+		+	—
Sphacelaria pennata	—	—	—	—	—	—	p	p	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	p	—	—
S. plumula	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	p
*Stictyosiphon soriferus**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—
S. tortilis	—	—	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tilopteris mertensii	—	—	—		—				—		—		—		—	—		—		—		—	—	—	—								—	—	—	—		—	+	—
Apoglossum ruscifolium	—	—	—	—	—	—	—	—	—	T	—	—	—	—	—	—	—	—	T	C	T	—	T	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—
Bonnemaisonia asparagoides	—	—					—		—	—						—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				+	—
B. hamifera sporoph.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	+	+
Brongniartella byssoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—
Callophyllis laciniata	+	+	+	—	—	—	—	—	+	+	—	+	—	—	—	+	+	+	+	+	+	—	+	—	+	+	—	+	+	+	—	+	+	+	+	—	—	—	—	—
Ceramium rubrum agg.	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	+	—	—

	Mar./Apr. 1958								July 1958								Oct. 1958								Jan. 1959								Apr. 1959							
	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Corallina officinalis	+	—		—	—																							—				—		—	—	—	—	—	—	—
Cruoria pellita	—	—	—	—	T			+	—	—	—	+	+	+	+	+	—			+	+	+		+		+		+	+	+	+		·	·		+	+	+	+	+
Cryptopleura ramosa	T	+	+	+	·	—	—	—	T	T	T	T	T	T	—	—	T	+	T	T	B	—	T	+	+	·	+	+	+	+		+	·	+	+	+	+	+		+
Delesseria sanguinea	·	+	+	+	—	·		·	·	—	·	—	+	·			·		+	+	·	·		—	T	T	T	+	·	+	·	+	·	·	·	+	+	·	—	·
Dilsea carnosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—													·						·			—	·		—	—
Dumontia incrassata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		·	—	—			—		—
Halarachnion ligulatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+			—
Heterosiphonia plumosa	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			—
Hypoglossum woodwardii	+	—	—	—	—	—	—	—	—	—	—	—	T	—	+	—	—	—	—	—	—	+	+	—	—	—	—	—	—	—	—	+	+	+	·	·	+	·	·	+
Lomentaria clavellosa	—	—	—	—	—	—	—	—	—	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	·		·	·		·	
L. orcadensis	—								·				·					—	—	—	·	·		—	—	—	—		—	·	·		T	T		—	·			·
Membranoptera alata	—	—	+	+	+	—	—	—	+	—	·	—	—	—	—	—	·	+	+	—	+	+		·	+	—	—	C	—		+		+	·	·	—	—		—	—
Nitophyllum agg.	—							—	B	T		B	B	T	·	·	—	—	—	—	·	·		—	—	—	·	—	+	·		—	—	—	—	+	+		—	
Odonthalia dentata	+	C	+					—	+	·	·	+	+	+	—	—	+	+	+	—	—	—	—	—	T	+	+	+	—	·	+	—	C	C	·	·	+	—	—	—
Phycodrys rubens	·	T	—	—	·	—	—	·	T	C	C	+	+	+	+	—	+	+	+	+	+	—	+	—	C	+	C	T	B		·	+	+	T		T	—	·	—	—
Phyllophora rubens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	·			·	·
Plocamium coccineum	T	+	T	—	—	—	—	—	+	+	—	—	—	—	—	—	T	+	+	—	+	—	+	+	+	—	—	—	—	—	—	—	—	+	+	—	—	—		·
Polysiphonia elongata	—	—	—	T	·	+	—	—	—	·	—	+	+	+	—	·	—		—	·	+	+	—		·	·	·		—	—	—	—	—		—	—	·	—	·	—
P. nigra	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				·	·	·		·
P. urceolata agg.	—	—				·					·		+	+			—	·	—	—	·	·	—	—					·			·	+	·		+	+	—	·	—
P. violacea agg.	—	—	—	—	+	S	—	T	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	S	—	—
Porphyrropsis coccinea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	·			—	·		—	·			·	·			·	·	—	·	—		+	·	—	—
Pterosiphonia parasitica	—	—	—	—	—	—	—	—	—	+	B	+	+	+	+	+	—	—	—	—	—	—	+	—	—	—	+	—	—	—	—	+	—	+	+	+	+	·	—	—
Ptilota plumosa	·	+	—	·	—	—	—	—	+	·	—	—	—	·	·	—		·	—	·		·	—	—	+	·		—	—	—	—	—	+		—	—	—	—	·	—
Rhodomela confervoides	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	·	—
Rhodophyllis divaricata	—	—	—	+	—	—	—	—	—	+	T	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	+	—	—	—	—	·	—	—	—	—	—	·	—
Rhodymenia palmata	+	+	—	—	—	—	—	—	+	+	—	—	—	—	—	—	+	+	—	—	—	—	—	—	+	—	—	—	—	—	—	—	+	+	—	—	—	—	·	—

* *Sensu* Naylor.

forest occupied the solid rock down to about 6 m, thinning out down to 8 m. The most important species within the forest were *Cryptopleura ramosa*, *Delesseria sanguinea*, *Cutleria multifida* sporophyte, *Phycodrys rubens* (mainly on *Laminaria* stipes), *Dictyota dichotoma* and *Pterosiphonia parasitica*. In the region of thinner forest and for some distance downwards on the boulders, *Saccorhiza polyschides* was dominant. Here the accompanying flora was similar, but *Dictyota* became gradually more abundant until it formed a practically complete cover of the outermost boulders. Most of the important species were common to both the solid rock or the boulders, with the exceptions of *Plocamium coccinium*, *Odonthalia dentata*, and *Phycodrys rubens* which occurred mainly on the rock, and of *Hypoglossum woodwardii*, *Polysiphonia elongata* and *Desmarestia aculeata* which occurred mainly on the boulders.

Surby Bowes Cave

Just north of Fleshwick Bay there is a narrow cave facing about north-west, with almost vertical sides and a sublittoral bottom of shingle and boulders sloping up from about 3 m below ELWS at the mouth to about 1 m at the inside end.

Two samples were taken in October 1959 (Table 1), one from the vertical end wall, at about 0 m, and one from an intermediate boulder, at about 1 m. In spite of the low light intensity at the former position, there were four species present. *Cryptopleura ramosa* was the most common but in an unusual form; a large proportion of the frond was polystromatic and some plants had tendrils. *Ptilothamnion* was present here: Dr Dixon found that the erect fronds of this were very variable in appearance, showing a complete range of intergrading forms between the typical *P. pluma* and *P. lucifugum*. *Cryptopleura* was the most abundant species on the boulder, where it took a number of forms.

The Sker

At the north-west corner of Port Erin Bay a reef runs out south-westwards from Bradda Head. The main rock of the reef has almost vertical sides from above high water down to about 8 m below ELWS, after which boulders form a gently sloping bed down to sand at 11 m. Just eastwards from this reef the floor of a small bay is occupied by a steeply sloping bed of large boulders, giving way to stones at 10 m and sand at 11 m. The outer part of the reef itself is subjected to a strong tidal stream, but the inner boulders are protected from this.

An incomplete series of algal samples was taken in May 1959 (Table 1). The *Laminaria hyperborea* forest extended down to 4 m on the vertical face and to 5 m on the large boulders eastwards. *Saccorhiza polyschides* was dominant on both sets of boulders in the region at and below the *Laminaria* limit down to about 7 m. Below that the boulders were bare of large algae, but the stones at 11 m bore *Dictyota dichotoma*, *Desmarestia aculeata*, *Cryptopleura ramosa*, *Delesseria sanguinea* and *Laminaria saccharina*. The reason for this colonization of the stones in preference to the rocks is not yet certain.

Port Erin Breakwater

During the last century the breakwater extending northwards from the south-west corner of Port Erin Bay collapsed and the large concrete blocks and boulders from which it was built now form an uneven ridge with its top at about mid-tide, sloping steeply on the inside (east) to sand at about 7 m below ELWS and sloping gently on the outside to sand with gravel in places at 9 m. The upper parts are formed only of concrete blocks about 2 m long, while the lower parts have boulders mixed with the blocks. Tidal streams are weak and effect only the top and end.

Sampling has been carried out at three-monthly intervals throughout a year on the outer (western) side. The records are given in Table 3. The *Laminaria hyperborea* forest was thick on the upper surface of the concrete blocks down to 5–6 m. At this level *Saccorhiza polyschides* dominated at all times of year. The most abundant smaller plants at all levels were *Cryptopleura ramosa*, *Delesseria sanguinea*, *Dictyota dichotoma*, *Phycodrys rubens*, *Cutleria multifida* sporophyte, *Desmarestia aculeata* and *Odonthalia dentata*. There was no marked change in the qualitative composition of the flora during the year, except for the apparently complete absence of *Dictyota* in January. That the disappearance of this species from sublittoral rocks in winter is a regular occurrence was confirmed the following year. The forms of many of the species showed a seasonal change, the fronds of such plants as *Delesseria* and *Odonthalia* becoming denuded in the autumn and regenerated in January. There was no suggestion of a summer annual flora. More species were recorded in April 1959 than April 1958; this may have been a reflexion of improved technique rather than a difference between the years.

Creg Liauyr

Between Port Erin breakwater and Bay Fine an exposed reef extends west-north-west from the shore. Beyond this, under water, there are a number of isolated rocky knolls with steep sides, surrounded by large boulders which slope steeply to the level of the gravel, at 13·5 m, where they stop abruptly. Just south-west of the reef the boulders are smaller, 1–2 m across, and slope more gently down to the gravel. The region is subjected to some tidal stream at springs but very little at neaps.

Two series of samples were taken, one ('north') on the rocky knolls and large boulders, and the other ('south') on the continuous boulder bed, in April–June 1958 (Table 1). In both places there was the usual thick forest of *Laminaria hyperborea* which faded out between 6 and 8 m below ELWS. Again *Saccorhiza polyschides* was most abundant at this level. The undergrowth flora in both places consisted mainly of *Phycodrys rubens* (mostly on *Laminaria* stipes), *Cryptopleura ramosa*, *Delesseria sanguinea*, *Dictyota dichotoma*, *Cutleria multifida* sporophyte, *Desmarestia aculeata*, *Odonthalia dentata*, *Pterosiphonia parasitica*, *Plocamium coccineum*, *Membranoptera alata* and *Callophyllis laciniata*. Most of these extended below the *Laminaria* forest for about 2 m but the *Cutleria* sporophyte was the principal occupier (though not forming a continuous cover) of the lowest boulders at 11–12 m. There was little difference between the main constituents of the flora of the two regions, but the smaller boulders south showed a greater variety in the more occasional species.

The Bowes

Between Bay Fine and Aldrick a rocky reef lies just off the shore, and is known as Halfway Rocks or the Bowes. Part of this is visible at all stages of the tide, but offshore from it there is an extensive submerged rock with its pinnacle at 5 m below ELWS. The gravel bed lies deeper here than nearer Port Erin, with the result that there are rocky surfaces down to 16 m below ELWS. The reef itself is very uneven with ledges, cliffs and overhangs. The reef is subjected to fairly strong tidal streams even at neaps.

The main sampling series was made in April–May 1958 (Table 2). The *Laminaria hyperborea* was as dense as found in the previous places mentioned, and thinned out between 10 and 12 m. Here again *Saccorhiza polyschides* formed a dominant zone at the lower limit of *Laminaria*. The associated flora was also similar. The similarity of the flora to that of the breakwater and Creg Liauyr is remarkable in that the whole spectrum is 4–5 m lower. The top of the Bowes rock is at the same level as the lower limit of *Laminaria* at the breakwater, but the forest is thick for another 5 m downwards. Some algae were present on the lowest rock surfaces at 16 m, though the cover was sparse; the most common were *Desmarestia aculeata*, *Delesseria sanguinea*, *Cutleria multifida* sporophyte, and *Heterosiphonia plumosa*. In December the only occupant of this level had been *Cutleria* sporophyte.

The Leods

Near the entrance to Calf Sound a reef known as the Heifer Rocks or the Leods lies offshore with its top just above LWS. The main shore is steep at this point, with some boulders at the base. The channel between here and the reef is narrow with a rocky bottom at about 10 m below ELWS. The side of this formed by the reef is slightly overhanging, while the south-western side of the reef is about vertical with a boulder bed at its base at 14 m, sloping gently down to the gravel at 17 m. The northern side of the reef is also a sloping boulder bed. The reef is subjected to strong tidal streams.

An incomplete series of samples was taken in July 1958 and 1959 (Table 2). *Laminaria hyperborea* extended to 6–10 m. The steep inner side of the reef was occupied by *Alcyonium* below about 3 m where it overhangs. The flora in the *Laminaria* forest had the usual composition, while the south-west boulders at 14 m were occupied mainly by *Dictyopteris membranacea*, *Dictyota dichotoma*, *Cutleria multifida* sporophyte, *Bonnemaisonia asparagoides* and *B. hamifera* sporophyte.

Spanish Head

Spanish Head lies on the other side of Calf Sound and consists of steep cliffs with large boulders (2–3 m across) below them under water. These slope steeply (at about 1 in 5) into deep water and provide the deepest rock so far encountered on the island at 22 m below ELWS. The Head is subjected to very strong tidal streams on both flood and ebb.

Sampling was first carried out in July 1959 (Table 2). The *Laminaria hyperborea* plants were large and the forest started thinning at about 9 m but extended to 14 m below ELWS. *Saccorhiza polyschides* extended over a wide range, down to 19 m, but was again probably most abundant at the lower limit of *Laminaria*. The main species occurring within the forest and some distance below it were *Cryptopleura ramosa*, *Phycodrys rubens*, *Plocamium coccineum*, *Cutleria multifida* sporophyte, *Pterosiphonia parasitica*, *Desmarestia aculeata*, *Dictyota dichotoma*, *Callophyllis laciniata* and *Nitophyllum* agg. Those confined to above 10 m were *Rhodymenia palmata*, *Callithamnion tetragonium* and *Porphyra umbilicalis* f. *rosea* (all on *Laminaria* fronds), *Desmarestia ligulata* and *Odonthalia dentata*. Below 10 m the vegetation became sparse and irregular; some of the boulders had a fair cover of small forms, some were bare and some were colonized by *Alcyonium*. From 10 to 18 m the most important species were *Bonnemaisonia asparagoides*, *B. hamifera* sporophyte and *Hypoglossum woodwardii*, in addition to those already mentioned. Below this the vegetation was very sparse indeed and a close search was necessary to detect it. Even so, there were still eleven species present on the lowest boulders at 22 m, the most important being *Antithamnion plumula*, *Bonnemaisonia hamifera* sporophyte, *Compsothamnion thuyoides*, *Pterosiphonia parasitica* and *Cutleria multifida* sporophyte. The crinoid *Antedon* occupied many of the boulders.

In February 1960 further sampling was carried out on the lower boulders in order to determine whether the sparse algal cover was confined to the summer. Although the vegetation was considerably reduced in quantity the majority of the species were still present (Table 2). The most marked absence was of *Dictyota dichotoma*, which also disappeared from other sublittoral rocks in winter. *Bonnemaisonia asparagoides* and *Compsothamnion thuyoides* had also apparently disappeared. Although it was almost too dark to read at the lowest depth, at least five species were still present. *Plocamium coccineum* was abundant at 19 m, where there was also a first year sporeling of *Laminaria hyperborea* (with mucilage canals in the stipe). This was the deepest record for this plant.

Scarlett Point

The shore just east of the southern tip of Scarlett Point is formed of limestone ledges, each ledge being inclined slightly upwards towards the sea. Sublittorally the configuration is very similar, though obscured by the thick forest of *L. hyperborea*. The general slope is very gentle and in places there are patches of gravel. There are also shallow gullies containing boulders.

An incomplete series of samples was taken in July 1959 (Table 2). The *Laminaria* forest was very thick. The rock below was noticeably bare, apart from a cover of *Lithothamnion* and small quantities of the usual species. Even *Cutleria multifida* sporophyte, the most regular species, was present in only very small amounts in the really thick forest at 1–5 m; its place was largely taken by *Cruoria pellita*. All these extended over the depth range sampled (the level of the gravel bed proper was not reached), except for *Odonthalia dentata* which ceased at 5 m. The boulders in the gullies were occupied by *Laminaria saccharina*.

Dreswick Point (Langness)

Langness is a narrow peninsula extending southwards and Dreswick Point is the southern tip of this. Offshore the tidal stream is notoriously strong, but there is little evidence of this inshore. Just west of the lighthouse a gully runs southwards, with boulders on its gently sloping floor and several steep-sided knolls of rock about 8 m high.

An incomplete series of samples was taken from a knoll and the boulders in July 1959 (Table 2). The knoll was occupied by *L. hyperborea* forest as usual, but the associated flora differed somewhat from that common near Port Erin: *Heterosiphonia plumosa* was the most prominent red alga, and neither *Cutleria multifida* sporophyte nor *Dictyota dichotoma* was recorded. The *L. hyperborea* extended to the bottom of the knoll, at 11 m below ELWS, with occasional plants on the boulders. There was no *Saccorhiza polyschides* zone, the boulders being occupied instead by *L. saccharina*. The level of the gravel bed was not reached, though there were patches of coarse sand amongst the boulders.

UNSTABLE BOTTOMS

Over the course of a number of years Lodge (1954) carried out a great many dredging operations around the south end of the Isle of Man and recorded a total of 128 species. Many of these have not been found on the rock surfaces, and as some of the areas which she dredged were gravel beds it seems likely that a considerable flora could develop on the unstable bottom under certain conditions. Little attempt has been made to extend these particular observations using diving equipment, but the few direct records on gravel that have been made (Table 4) may be of interest. It must be emphasized that these algae were attached to superficial stones and were clearly not drifting.

Glen Maye Bay

Glen Maye Bay, just north of Niarbyl, was sampled in July 1959. The bottom consists of small boulders and stones mixed with gravel. At 11 m below ELWS the gravel (diameter 2–30 mm) bore *Chorda filum*, *Brongniartella byssoides*, *Myriocladia?* sp., *Stictyosiphon tortilis*, *Cutleria multifida* gametophyte (male and female), *Sporochnus pedunculatus*, *Cladostephus spongiosus*, *Acrothrix gracilis* and other species. This assemblage clearly differed from those found on the rock reefs. Brown algae were predominant. Further offshore, at 12 m, there were small boulders and these bore many of the species normally inhabiting rock surfaces: *Saccorhiza polyschides*, *Dictyota dichotoma*, *Halidrys siliquosa*, *Heterosiphonia plumosa*, *Cutleria multifida* sporophyte, *Hypoglossum woodwardii*, *Brongniartella byssoides*, *Pterosiphonia parasitica* and *Phycodrys rubens* being the most common.

Stroin Vuigh

In July 1959 the lowermost boulders (10 m) at Stroin Vuigh, already described, bore a flora very similar to that on the Glen Maye boulders. In addition, the gravel between the boulders was occupied by *Myriocladia?* sp., *Chorda filum*, *Enteromorpha clathrata* and *Cutleria multifida* gametophyte. *Myriocladia?* sp. was also found by Parke (private communication) in this region and then ascribed by her to *M. loveni* J. Ag. This was later found to differ from the Swedish material of this species (Parke 1950). Its identity is not yet certain.

Off Bradda Hill

In September 1958 small stones at 15 m below ELWS off the Charran, west of Fleshwick Bay, were occupied by *Brongniartella byssoides*, *Saccorhiza polyschides* sporelings and *Plocamium coccineum*. At 21 m the bottom was sand and gravel and there were no algae.

In August 1959 an extensive search was made at 32 m and at 23 m on the coarse gravel bed off the West Bradda Mines, but no attached algae were found. The calm sunny summer would have resulted in there being growth, given a spore supply, if this were ever possible, but clearly either the depth or tidal streams prevented it.

Off Creg Liauyr

Again in August 1959, somewhat shallower beds off Port Erin breakwater between Bradda Head and Bay Fine, where the tide is less strong, were found to support a fairly rich flora. The most abundant species, on stones of 5–20 cm, mixed with coarse sand, were *Saccorhiza polyschides*, *Stictyosiphon tortilis*, *Sporochnus pedunculatus*, *Arthrocladia villosa*, *Desmarestia aculeata*, *Cutleria multifida* gametophyte, *Bonnemaisonia asparagoides*, *Antithamnion plumula*, *Halarachnion ligulatum* and *Scinaia furcellata*. The gravel at 13 m adjacent to the boulders at Creg Liauyr was found in September 1958 to bear *Scinaia*, *Halarachnion*, *Antithamnion sarniense* and *Sporochnus pedunculatus*.

The same position was visited during the winter, at the end of November 1959, and the flora found to be almost negligible. Clearly the intervening gales had destroyed most of the plants which were dependent on the unstable bottom not being extensively disturbed.

TABLE 4. THE SPECIES OCCURRING IN SAMPLES FROM UNSTABLE BOTTOMS, AT VARIOUS DEPTHS

(+ = present; T = tetrasporangia; C = cystocarps; B = both; S = spermatangia; M = monospores; O = oogonia; A = antheridia; b = both; P = plurilocular and U = unilocular sporangia; p = propagules.)

	Glen Maye Bay, July 1959					Stroin Vuigh, July 1959				Off Charran, Sept. 1958			Off Creg Liauyr 1959			
													Aug.			Nov.
Depth (m below ELWS)	10	11	12	13	14	8	9·6	9·9	10	11	15	21	14	15	15·3	16
Cladophora sp.	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Enteromorpha clathrata (sensu Bliding, 1944)	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Ulva lactuca	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–
Acrothrix gracilis	U	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arthrocladia villosa	–	–	–	–	–	–	–	–	–	–	–	–	–	U	U	–
Chorda filum (sensu Hamel 1931–9)	+	–	–	–	–	–	–	+	–	–	–	–	+	+	–	–
Cladostephus spongiosus (sensu Hamel 1931–9)	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cutleria multifida gametophyte	b	–	–	–	–	–	–	+	–	–	–	–	A	+	+	–
C. multifida sporophyte	–	+	+	+	–	+	+	–	+	–	–	–	–	–	–	–
Desmarestia aculeata	+	–	–	–	–	+	–	–	+	+	–	–	+	+	+	–
Dictyota dichotoma	–	A	+	+	+	+	b	–	O	+	–	–	–	–	+	–
Ectocarpus confervoides	+	–	–	P	–	–	+	–	–	–	–	–	–	–	–	–
Halidrys siliquosa	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–
Laminaria saccharina	–	+	+	–	–	–	–	–	+	+	–	–	–	–	–	+
Myriocladia? sp. (see Parke, 1950)	U	–	–	–	–	–	U	U	–	–	–	–	–	–	–	–
Saccorhiza polyschides	+	+	+	–	–	+	+	–	+	+	+	–	+	+	+	+
Sphacelaria bipinnata	–	–	–	–	PU	–	–	–	–	–	–	–	–	–	–	–
S. pennata	p	–	p	–	–	–	p	–	p	–	–	–	–	–	–	–
S. plumula	–	–	–	–	–	p	–	–	p	–	–	–	–	–	–	–
Sporochnus pedunculatus	+	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–
Stictyosiphon tortilis	+	P	–	–	–	–	–	–	–	–	–	–	–	+	+	–
Antithamnion plumula	–	–	–	–	–	–	–	–	–	–	–	–	B	C	+	–
Bonnemaisonia asparagoides	–	C	C	–	–	–	–	–	C	–	–	–	C	C	C	–
Brongniartella byssoides	+	S	T	+	–	T	T	–	C	–	C	–	–	–	–	–
Callithamnion corymbosum	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Ceramium rubrum agg.	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chylocladia verticillata	–	C	T	–	–	–	–	–	–	–	–	–	–	–	–	–
Corynospora pedicellata	–	M	M	–	–	–	–	–	–	–	–	–	–	–	–	–
Cryptopleura ramosa	–	+	+	–	T	T	T	–	T	+	–	–	–	+	+	–
Delesseria sanguinea	–	–	+	–	–	+	+	–	+	+	–	–	–	–	–	–
Halarachnion ligulatum	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–	–
Heterosiphonia plumosa	–	+	+	+	–	–	+	–	+	–	–	–	–	–	–	–
Hypoglossum woodwardii	–	+	T	T	–	+	B	–	B	–	–	–	–	–	–	–
Lomentaria clavellosa	–	–	–	–	–	–	–	–	–	–	–	–	–	C	–	–
Membranoptera alata	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Nitophyllum agg.	–	T	T	–	–	B	B	–	T	–	–	–	+	–	–	–
Odonthalia dentata	–	+	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Phycodrys rubens	–	+	+	+	+	–	–	–	–	–	–	–	+	–	–	–
Plocamium coccineum	–	–	–	–	–	–		–	–	+	+	–	–	–	–	+
Polysiphonia brodiaei	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
P. elongata	–	+	–	–	–	+	+	–	+	–	–	–	+	+	–	–
P. urecolata agg.	–	–	S	–	–	–	–	–	–	–	–	–	–	–	–	–
P. violacea agg.	C	–	+	–	–	T	–	–	–	–	–	–	T	–	–	–
Pterosiphonia parasitica	–	+	+	+	–	+	+	–	+	–	–	–	–	–	–	–
P. thuyoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Ptilota plumosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Rhodomela confervoides	–	+	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Scinaia furcellata	–	–	–	–	–	–	–	–	–	–	–	–	C	+	–	–
Sphondylothamnion multifidum	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–

DISCUSSION

The aim of a preliminary survey of this nature is the recognition of the ecological problems peculiar to the habitat. The first that arises here concerns what was undoubtedly the most ubiquitous sublittoral plant, the sporophyte of *Cutleria multifida* (*Aglaozonia parvula*). It occurred at virtually every level sampled in all the localities except Langness, on rocky bottoms and on boulders though not on smaller stones. It rarely formed a continuous carpet, but patches could be found on almost all rocks, sometimes several layers thick. Occasionally it was mixed with prostrate *Dictyota dichotoma* but was easily distinguishable from this in transverse section. During the first year of sampling no gametophytes were found. The widespread occurrence of the other generation of the plant was therefore an enigma. Although alternation of generations is supposed to occur, by-passing of the gametophytic stage by the production of an *Aglaozonia*-like phase by zoospores from the sporophyte has been reported (Church, 1898). It was therefore thought likely that this might be the normal occurrence in these waters, and when a reproducing thallus was found on Port Erin breakwater in January 1959 it was kept under observation in the laboratory. The liberation of the spores was induced in culture medium. After 2 weeks they developed into branched filaments floating on the surface. A number of these were washed and transferred to fresh medium where, without exception, they developed into the gametophytic phase; these developed sporangia while still quite small, there being both male and female plants. Later that year gametophytes were first found in the field on Perspex slides which had been left out for some weeks; this suggested that a search of different habitats might reveal the gametophytes, at least during certain seasons. This proved to be so when they were found both in Glen Maye Bay and off Creg Liauyr (Table 4) during the summer. They had disappeared from the latter position by November. It therefore seems likely that the gametophytic stage of this plant exists as a transient population on the extensive gravel beds during the summer, when the relatively calm weather renders this substratum habitable, and then releases sufficient gametes to maintain the existence of the sporophytic phase on the rock surface. Amongst the limited number of gametophytic plants encountered in nature and culture there was no suggestion of a shortage of males as reported by Feldmann (1957) and others.

The second main problem arising is that of zonation. It is apparent that what zonation there is on the rock faces is determined not only by absolute depth but also by the level or proximity of the adjacent gravel bed. This is associated with the distribution of *Laminaria hyperborea*. As this plant is at present the subject of study it will not be further discussed here.

On solid rock and large boulders it is clear that when the absence of *L. hyperborea* allows, the growth of *Saccorhiza* takes place. It is present in some places mixed in with the former species in the forest, but it has its climax in the zone just below the *Laminaria* limit, where the light is evidently still sufficient for it but where the factor which limits *Laminaria* is evidently ineffective against it. It is probable that through its power of faster growth it can take advantage of transiently good conditions and become established, but because the plants are much less strongly constructed they last for a shorter time. It is worth stressing that the level of *Saccorhiza* dominance is dependent on the level of the *Laminaria*, at whatever depth this is.

The species forming the undergrowth of the *Laminaria* forest are not confined to that region and all extend downwards. The cover gradually becomes thinner, and near to the limit of the rock there are large patches of uninhabited surface. At the breakwater this bare zone is at the same depth as the rich forest flora of the Bowes or Spanish Head. This is in contrast to the situation in the Mediterranean, where Drach (1948*a*) insists that cover is always 100%; where the rock is not occupied by plants it is colonized by animals. It seems that some factor associated with the proximity of the gravel, which inhibits the establishment of algae, also acts on the animals. Where light alone is the limiting factor, on overhangs and possibly the deeper rock at Spanish Head, the place of algae may be taken by *Alcyonium* and sponges.

The presence of a number of algae on the lowest known rock at the darkest time of the year makes the determination of the general lower algal limit for the area impossible.

Thirdly, there arises the question of the effect of depth on reproduction. Jones (1956) suggested that the greater paucity of fertile species at the greater depth of 25 m at Bardsey might reflect a weaker ability to reproduce nearer the limit of the range of a plant, but this cannot be supported by the present records. The reason might be that in most cases in the Isle of Man the lower limit of sublittoral algae is determined by a factor acting not on the growth rate (such as light) but on initial establishment (such as the proximity of the gravel). A second suggestion made by Jones was that carposporic plants of *Brongniartella byssoides* and *Lomentaria clavellosa* grew deeper than tetrasporic plants; this was however based on single samples. All the available records in the present work have been examined with this in mind, but only *Brongniartella* showed any indication of a relationship between reproductive phase and depth. With this species, as at Bardsey, gametophytic plants were confined to deeper water, below 10 m, though there were only three records. There were 6 records of tetrasporic plants and only one of these was deeper than 10 m. This lends support to Jones's evidence.

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SUMMARY

A general survey has been made of the distribution with depth of the main sublittoral algae inhabiting the rock surfaces at ten places around the south end of the Isle of Man, using an aqualung. The region is characterized by the lack of any deep water rock; this is replaced by gravel at a depth of about 12 m in most places. Immediately below ELWS the vegetation was dominated by *Laminaria hyperborea*, forming a thick forest with an undergrowth of smaller brown and red algae. The lower limit of this forest was well defined, and depended not on the absolute depth but on the proximity of the junction of solid rock and the gravel bed. *Saccorhiza polyschides* dominated just below the *Laminaria hyperborea* limit, at whatever depth this was. The smaller algae of the forest extended down on the deeper rock but the cover was reduced as the gravel was approached. Observations were made on one reef throughout the year. Although the abundance and form of the more important species varied, most were present at all times of the year, but *Dictyota dichotoma* was absent in winter. The deepest rock found, at 22 m below ELWS, was colonized by a few algae even in winter. The most ubiquitous plant on the rock was the sporophyte of *Cutleria multifida* which appeared to alternate with sexual plants which formed part of a transient summer population of algae which occupied the gravel bed in places.

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CODIUM AMPHIBIUM: A SPECIES OF DOUBTFUL VALIDITY

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(Text-figs. 1–3)

Codium amphibium was described by Harvey (1844) on the basis of material sent to him by David Moore, who in turn had received it from the collector, William M'Calla. This material was said to grow 'on turfy banks at extreme high-water mark, near Roundstone, county Galway', and was described as comprising numerous erect, small (to $\frac{1}{4}$ in. high), simple, cylindrical or subclavate, obtuse fronds arising from a mass of entangled, divaricately branched filaments densely aggregated into widely spreading patches. Harvey's illustration clearly shows the habit, but his drawing of utricles is neither diagnostic nor accurate [as judged from our study of the type material]. Harvey made particular note of the habitat, which he inferred would place the plant 'beyond the reach of the ordinary sea-level'. In a later work, Harvey (1846, pl. 35B) illustrated this species with similar drawings and added nothing to the description except to extend the maximum height of the fronds to 'nearly half an inch'. Still later, Harvey (1849, p. 194) increased the maximum height of the fronds to an inch, modified 'simple' to 'usually simple, rarely emarginate or forked', added the locality 'at the head of Birtirbui Bay, Galway' and changed the habitat as follows: 'Turf banks, near high-water mark, but washed by every tide...' Kützing (1849, p. 502) furnished a description similar to the original one, based on an Irish specimen sent to him by Berkeley, probably topotype material*. In his illustration of this material, Kützing (1856, pl. 96, fig. á) showed an important character of the utricles: a tendency towards pointed apices.

The first report of *C. amphibium* from some locality other than Ireland was that of Tellam (1883), who collected what he considered to be this species at Falmouth in 1882, growing on a small ledge of rocks near high-water mark to the west of Pendennis Castle, sheltered by higher rocks on the south, but covered by every tide. The fronds were said to be $\frac{1}{4}$–$\frac{3}{8}$ in. high, arising from patches of glossy, dark green filaments which spread through and on the muddy sand covering the rocky ledge. J. Agardh (1887), in his monograph of *Codium*, placed *C. amphibium* in his tribus *Codii tomentosi*. Holmes & Batters

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* The three specimens of *C. amphibium* in Kützing's herbarium at Leiden are labelled 'Roundstone Bay', 'Ireland. Harvey. Herb. Kützing' and 'Connemara. Andrews,' respectively.

(1890, p. 77) reduced *C. amphibium* to the status of a form of *C. adhaerens*. Batters (1902, p.22) listed the Isle of Man as an additional locality for *C. amphibium* on the basis of material from Perwick Bay collected by George in 1890. Cotton (1912, p. 113) reported finding this species on a ledge at the mouth of a cave on Clare Island in 1909 and 1911. He also reported that a special search for the plant at Roundstone during September 1911 was without success. Schmidt (1923) included *C. amphibium* in his monograph of the genus solely on the basis of previously published accounts, but in 1939, after having had the opportunity to study material from Port-en-Bassin [Calvados, France, reported earlier by Fortin (1935) as an unnamed variety of *C. tomentosum*] in addition to topotype material from Roundstone, he published a supplementary account of the species. The following secondary references complete the literature for *C. amphibium*: Cocks (1853, p. 77); Gifford (1853, p. 289); Harvey (1857, p. 159, pl. 62, fig. 289); Johnstone & Croall (1860, p. 5); Gatty (1863, p. 123); Gray (1867, p. 243); DeToni (1889, p. 491); Knight & Parke (1931, p. 55); Newton (1931, p. 105); Parke (1953, p. 500).

The amount of information available about *C. amphibium* is not commensurate with the number of published accounts. Up to now neither hairs nor gametangia have been observed. During the last few years one of us (Silva) has had an opportunity to study collections assigned to this species in the major herbaria of the world in addition to liquid-preserved material from Falmouth and from St Andrews, kindly provided by Dr M. A. Wilson and Dr Irvine, respectively. The other of us (Irvine) has been keenly interested in the problem of *C. amphibium* because plants suggestive of this species were growing in tide pools that were the object of an ecological study.

An examination of the type collection in Trinity College, Dublin, confirmed the presence of pointed utricles (Fig. 1, A), as shown first by Kützing (1856) and later by Schmidt (1939). Juvenile plants of *C. fragile* subsp. *atlanticum* (Cotton) Silva are immediately called to mind, and it may be noted that a similar impression was gained by W. A. Setchell from his study of topotype collections of *C. amphibium*. In a letter to A. D. Cotton, dated 10 June 1930, Setchell wrote, 'In all probability this species is simply a depauperate form of your variety [*C. mucronatum* var. *atlanticum*]'. In agreement with the type collection are all topotype collections that we have examined (Fig. 1, B) as well as the Cotton specimens from Clare Island (Fig. 1, C), the George specimens from the Isle of Man (Fig. 1, D), and a collection from Tellam's site near Falmouth (M. A. Wilson, viii.1943; Fig. 2, D).

An opportunity to learn more about *C. amphibium* was provided by the discovery by Dr Helen Blackler at St Andrews of plants referable to this species growing on the vertical sides and the bottom of a few rock pools on the Hind Rock and a neighbouring ridge at M.H.W.N.T. towards M.H.W.S.T. They were first observed in November 1949 and subsequently have been followed

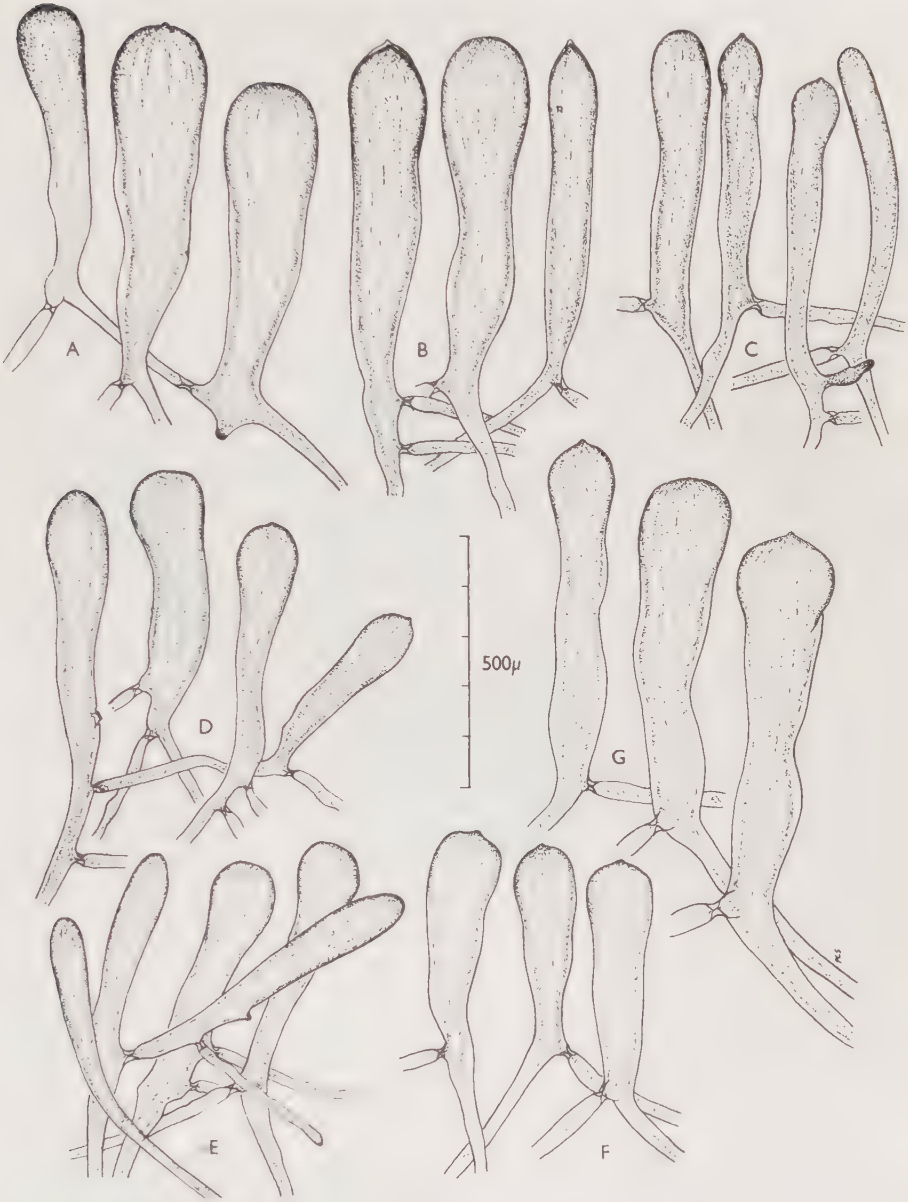

Fig. 1. Utricles from erect fronds (samples taken about 3 mm below tip). A–D, *Codium amphibium.* A, Roundstone Bay, *M'Calla*, TCD = type; B, Connemara, *M'Calla*, K; C, Portlea, Clare Island, viii. 1911, *Cotton* 358, K; D, Perwick Bay, Isle of Man, 3. ix. 1890, *George*, BM. E–G, *Codium fragile* subsp. *atlanticum.* E, St Andrews, 18. ix. 1952, *Irvine*, liquid-preserved in UC, frond 5 mm high; F, St Andrews, xi. 1955, *Blackler*, UC, frond 4 mm high; G, St Andrew, 5. x. 1955, *Blackler*, UC, frond 14 cm high.

from year to year. The erect fronds arising from the vaucherioid mat at first were mostly simple, a few being once-forked. In the autumn of 1953 repeatedly branched thalli developed to a height of 3·5 cm, and in 1955 to 15 cm (Fig. 3). The fronds which developed in 1959 reached a height of 28 cm and bore gametangia. The utricles showed progressive changes from 1949: at first, they had rounded apices (Fig. 1, E); later, they were identical with those of *C. fragile* subsp. *atlanticum* (Figs. 1, F and G). The conclusion is drawn that *C. amphibium* at St Andrews is merely a juvenile stage of *C. fragile* subsp. *atlanticum*. Blackler (1956), in collaboration with us, reached the same conclusion. It seems reasonable to suppose that the Irish *C. amphibium* has a similar status, although in the absence of direct proof it must be admitted that

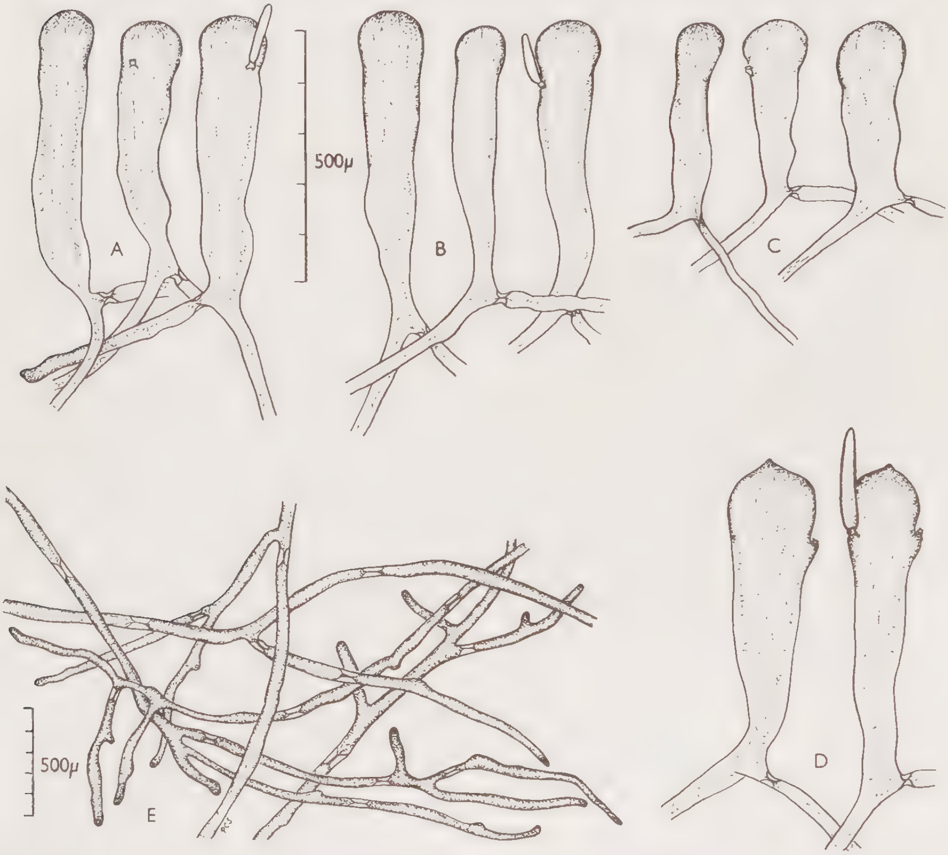

Fig. 2. A–D, utricles from erect fronds (drawn to upper scale). *Codium 'amphibium'* [= juvenile stages of *C. tomentosum*]: A, Falmouth, *Holmes*, BM; B, Elberry Cove, 14. ix. 1954, *Wilson*, liquid-preserved in UC; C, Port-en-Bassin, *Fortin*, PC. *Codium fragile* subsp. *atlanticum*: D, Falmouth, viii. 1943, *Wilson*, liquid-preserved in UC. E, vaucherioid filaments at base of frond figured in D (drawn to lower scale).

it could be a non-sexually reproducing series of populations maintained in a juvenile stage by the operation of environmental factors related to the purported amphibious habitat.

The development of extensive mossy vaucherioid growths of unconsolidated filaments (Fig. 2, E) is characteristic of members of the Codiaceae (Taylor, Joly & Bernatowicz, 1953). In *Codium* they represent juvenile stages, although not all species, nor all plants of a given species, seem to develop in this manner. Many fronds apparently arise from a spongy crustose base rather than from a vaucherioid mat, although it is possible that in these instances earlier vaucherioid stages have been overlooked. Morphogenesis in *Codium* has scarcely been studied and holds much promise for future investigation.

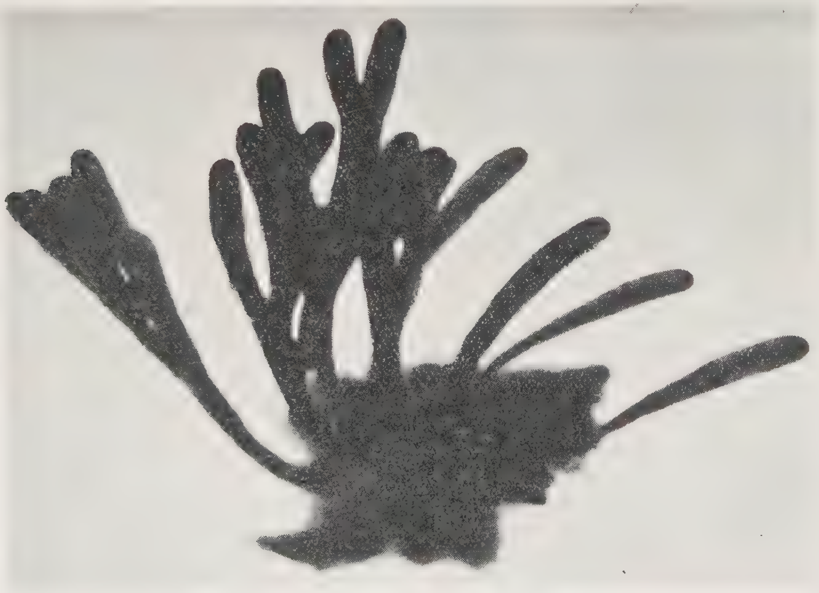

Fig. 3. *Codium fragile* subsp. *atlanticum*, St. Andrews, 1957. Photo: Dr Helen Blackler.

A study of some other material agreeing in habit with *C. amphibium* has revealed that *C. tomentosum* also has a vaucherioid juvenile stage. Several collections from Falmouth by Tellam and by Holmes (Fig. 2, A), the one by Fortin from Port-en-Bassin (Fig. 2, C), and one by Dr M. A. Wilson from Elberry Cove, Torbay, Devon (Fig. 2, B) are all referable to *C. tomentosum*.

We are grateful to the directors and curators of the following herbaria for the opportunity to study critical specimens: British Museum (Natural History) (BM); Royal Botanic Gardens, Kew (K); Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris (PC); Trinity College, Dublin (TCD). We wish to thank Dr M. A. Wilson, Dr Mary Parke, and Dr Helen Blackler for their interest and valuable help in this study.

SUMMARY

Plants agreeing in habit with the material originally described as *Codium amphibium* have been shown to be juvenile stages of *C. fragile* subsp. *atlanticum* and *C. tomentosum*. The type specimen is probably a juvenile of the former species. *C. fragile* subsp. *atlanticum* is reported for the first time from Cornwall.

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EXCHANGES OF WATER BETWEEN THE ENGLISH AND BRISTOL CHANNELS AROUND LANDS END

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(Text-figs. 1–11)

An understanding of the oceanography of the Celtic Sea requires an understanding of the exchanges of water around four headlands, Ushant, Lands End, St Davids Head and Carnsore Point. As a sequel to the study on the flow past Ushant already presented (Cooper, 1960*b*), this paper and the following one by Cooper, Lawford & Veley are attempts to achieve a better understanding of the exchanges around Lands End and in the neighbourhood of the Scilly Isles (Fig. 1).

Matthews (1914, p. 20) said: 'The charts published in this report show that the saltest water enters the Irish area between Lands End and the Scilly Islands, and detailed observations made along this line on several cruises at intervals of from half a mile to one mile on the Marine Biological Association's steamers have shown that the axis of highest salinity lies midway between the Longships Rock and the Seven Stones Lightship, that is, at a distance of only a few miles off Lands End. This current of salt warm water is derived from a current which has already entered the English Channel from a south-westerly direction, and has in part turned northwards and north-westwards to escape into the Irish Channel. It is practically certain that this water has come from the mouth of the English Channel and not directly from the open sea because further westwards a great area of lower surface salinity stretches southwards across the fairway and prevents any such direct current.'

Harvey (1925, fig. 19) accepted Matthews' interpretation and later (1929) from a study of geopotential topographies deduced that a residual current ran between Lands End and the Scillies in June 1924 in a N.N.E. direction with a velocity of about $1\frac{1}{2}$ miles per day compared with the water at 60 m. Carruthers (1934) suspected that N.N.E. may be a misprint for N.N.W. but both descriptions could be applied to different parts of the course sketched; N.N.E. applies more nearly in the passage itself.

The current measurements of Carruthers, Lawford & Veley (1951) further discussed in the following paper (Cooper, Lawford & Veley, 1960) cannot be gainsaid but appeared gravely to conflict with the deductions of Matthews and of Harvey.

Lumby (1935, p. 33) also remarked that 'an area of small extent (in the neighbourhood of the 'Seven Stones') appears to have a different régime from the rest of the Channel, according to the fluctuations of salinity from year to year. The same probably applies also to the seasonal variation.' Lumby & Carruthers *et al.* are thus in agreement. If measurements of current, temperature and salinity at the Seven Stones Light Vessel are considered to represent the whole of the Lands End–Scilly passage, we have no choice but to reject the deductions of Matthews and Harvey.

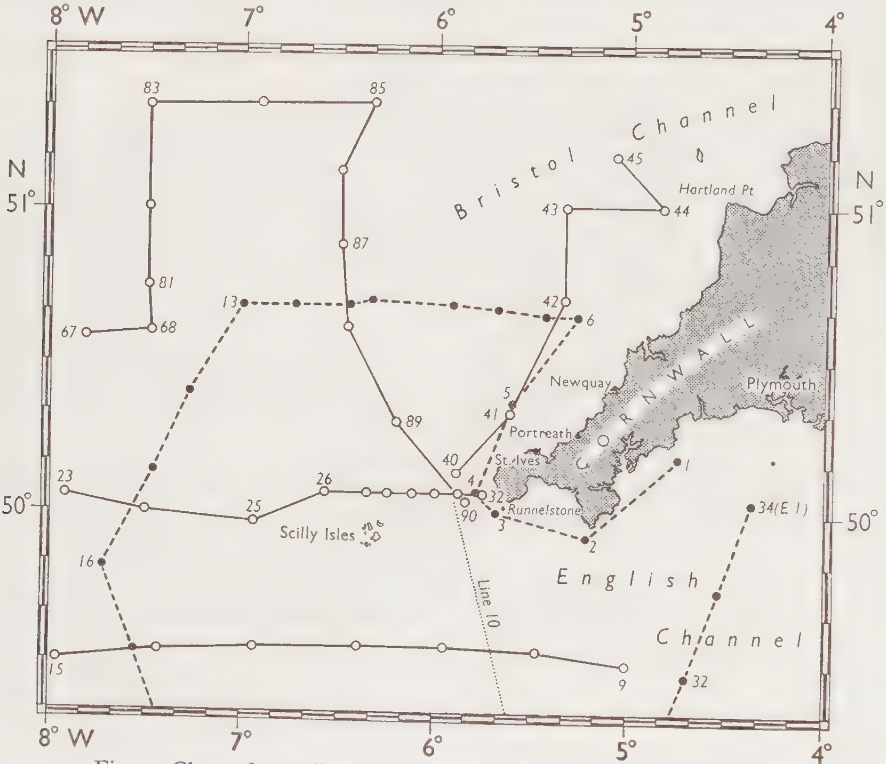
8° W
7°
6°
5°
4°
N
51°
50°
Bristol Channel
Hartland Pt
CORNWALL
Newquay
Portreath
St. Ives
Runnelstone
Plymouth
Scilly Isles
English Channel
Line 10
83
85
87
81
68
67
89
13
6
42
43
44
45
5
41
40
4
32
90
3
2
1
34(E 1)
32
23
26
25
16
15
9

Fig. 1. Chart of area discussed and stations worked in April (full lines) and June 1950 (pecked lines).

The conflict may be resolved if we assume, as Matthews implied, that measurements at the light vessel may not be representative of the whole width of the passage and that a narrow corner current with other characteristics may flow snugly around Lands End from the south coast to the north coast of Cornwall. This was the state of our knowledge when our 1950 cruises were planned. The results, as first appreciated, were equivocal.

But let us start by examining the observations of salinity and temperature at the Seven Stones Light Vessel; as observations, these have quite exceptional homogeneity and apparent reliability.

TABLE 1. THE MEAN TEMPERATURE AND SALINITY IN REGION 5 (= SEVEN STONES LIGHT VESSEL) FOR MONTHS AND YEARS OF THE PERIOD 1928–58

Continuation of Lumby (1935; Table 16)

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year mean
							Temperature						
1928	10·29	9·75	9·85	10·62	12·15	13·06	15·74	16·42	15·74	14·19	12·51	11·09	12·62
1929	9·86	9·59	9·29	9·94	10·81	13·35	14·26	16·36	16·28	13·78	12·06	10·52	12·18
1930	9·95	9·19	9·09	9·78	11·30	14·20	15·36	15·00	14·91	13·45	12·48	11·19	12·16
1931	10·14	9·19	8·75	9·72	10·72	13·39	15·24	14·75	14·21	13·75	12·52	11·64	12·00
1932	10·72	9·74	9·46	9·51	10·62	14·22	15·45	17·62	16·31	13·18	12·19	11·19	12·52
1933	10·36	9·54	9·59	10·36	12·00	13·74	16·50	17·28	16·11	14·24	12·38	10·80	12·74
1934	10·01	9·32	9·14	9·25	10·44	14·70	16·96	15·74	14·76	13·32	11·91	11·22	12·23
1935	10·28	9·65	9·38	9·89	10·55	12·32	15·49	16·59	14·86	13·36	11·99	10·61	12·08
1936	9·90	9·58	9·60	10·26	11·30	13·82	15·19	15·31	16·19	13·95	12·55	11·08	12·39
1937	10·21	9·84	9·28	9·79	11·66	14·38	15·80	17·70	15·65	13·64	12·21	11·00	12·60
1938	10·00	9·38	9·48	9·88	10·90	12·65	13·98	15·38	14·28	13·56	12·85	11·22	11·96
1939	9·99	9·52	9·09	9·62	10·92	13·59	14·51	15·20	15·66	13·21	—	—	—
1940–46	—	—	—	—	—	—	—	—	—	—	—	—	—
1947	—	—	—	—	10·71	12·68	14·61	17·49	17·34	14·65	13·61	12·00	—
1948	10·72	9·75	9·95	10·18	11·74	13·14	13·89	16·01	14·79	14·01	12·84	11·89	12·41
1949	10·70	10·26	10·14	10·45	11·38	14·22	16·86	17·39	17·19	15·60	13·29	11·90	13·28
1950	10·94	10·01	10·11	10·35	11·09	14·38	16·08	16·35	15·26	13·59	12·41	10·40	12·58
1951	9·68	9·14	8·80	9·24	10·20	12·58	15·49	15·84	14·50	13·74	12·91	11·61	11·98
1952	10·38	9·08	9·36	10·00	11·96	13·49	15·48	15·74	14·86	13·04	11·90	11·00	12·19
1953	9·82	9·16	9·18	9·62	11·01	13·00	15·34	16·34	15·34	14·02	12·52	12·19	12·30
1954	11·10	9·94	9·68	10·04	10·85	13·15	14·05	14·79	14·56	13·99	12·54	11·28	12·16
1955	10·59	9·28	8·68	9·11	10·50	12·60	16·19	17·68	16·48	13·69	12·39	11·82	12·42
1956	10·70	9·45	8·95	9·54	10·72	13·09	14·19	15·21	13·80	13·41	12·30	11·42	11·90
1957	10·29	9·60	9·86	10·50	11·44	14·02	15·86	15·60	15·14	13·54	12·19	11·10	12·43
1958	10·16	9·72	9·49	9·98	11·76	13·64	15·25	15·80	16·40	14·62	13·80	12·74	12·78
							Salinity						
1928	35·341	35·404	35·309	35·330	35·174	35·086	35·291	35·214	35·161	35·232	35·178	35·219	35·245
1929	35·221	35·270	35·278	35·329	35·256	35·232	35·298	35·125	35·234	35·251	35·165	35·154	35·234
1930	35·232	35·250	35·331	35·269	35·321	35·336	35·304	35·106	35·261	35·221	35·184	35·219	35·253
1931	35·190	35·069	35·206	35·305	35·295	35·260	35·238	35·178	35·159	35·211	35·270	35·342	35·227
1932	35·235	35·294	35·384	35·362	35·370	35·385	35·255	35·229	35·184	35·289	35·371	35·322	35·307
1933	35·379	35·404	35·414	35·349	35·312	35·248	35·278	35·198	35·171	35·309	35·416	35·394	35·323
1934	35·530	35·502	35·452	35·526	35·420	35·425	35·338	35·461	35·378	35·376	35·366	35·352	35·427
1935	35·325	35·286	35·326	35·345	35·391	35·288	35·365	35·294	35·262	35·281	35·226	35·218	35·300
1936	35·215	35·221	35·008	34·840	34·826	34·864	34·821	34·952	34·966	35·162	35·191	35·180	35·020
1937	35·149	35·110	35·096	35·209	35·264	35·269	35·232	35·268	35·145	35·222	35·301	35·325	35·216
1938	35·275	35·259	35·264	35·310	35·349	35·296	35·306	35·296	35·301	35·171	35·230	35·188	35·270
1939	35·211	35·298	35·199	35·184	35·274	35·341	35·226	35·166	35·219	35·266	—	—	—
1940–46	—	—	—	—	—	—	—	—	—	—	—	—	—
1947	—	—	—	—	35·334	35·286	35·171	35·125	35·029	35·206	35·349	35·324	—
1948	35·301	35·269	35·396	35·304	35·389	35·334	35·266	35·145	35·191	35·221	35·345	35·289	35·288
1949	35·248	35·259	35·249	35·136	35·112	35·159	35·254	35·229	35·200	35·155	35·216	35·184	35·200
1950	35·136	35·270	35·206	35·155	35·159	35·169	35·155	35·282	35·106	35·105	35·171	35·152	35·172
1951	35·131	35·174	35·175	35·278	35·294	35·285	35·322	35·234	35·208	35·298	35·366	35·350	35·260
1952	35·282	35·231	35·218	35·340	35·269	35·250	35·201	35·214	35·241	35·265	35·335	35·369	35·268
1953	35·321	35·326	35·385	35·341	35·295	35·318	35·121	34·961	34·978	35·122	35·325	35·291	35·232
1954	35·299	35·274	35·284	35·205	35·248	35·215	35·134	34·899	34·985	35·040	35·152	35·111	35·154
1955	35·202	35·158	35·218	35·238	35·148	35·096	34·994	34·995	35·122	35·165	35·264	35·290	35·158
1956	35·260	35·265	35·278	35·275	35·245	35·101	34·998	34·926	35·214	35·249	35·312	35·271	35·200
1957	35·259	35·225	35·162	35·151	35·252	35·221	35·219	35·149	35·084	35·151	35·135	35·174	35·182
1958	35·217	35·208	35·089	35·229	35·195	35·191	35·216	35·094	35·068	35·222	35·254	35·339	35·194

Temperature and salinity at the Seven Stones Light Vessel, 1928–58

The light vessel is moored in about 40 fm. of water about 2 miles north-eastward of the Seven Stones, about 14 miles west of Lands End and immediately south of station 29 in Fig. 1. After sporadic observations from May 1903, systematic observations were started in October 1905, at the rate of four per month. In 1912 observations every 4 days were initiated and this level of sampling has been maintained except for a break from 17 October 1939 to 16 March 1947. They provide a base to which all other observations in the area may be referred and are maintained by the Fisheries Laboratory, Lowestoft.

The observations up to 1927 have been very thoroughly reviewed by Lumby (1935) who treated the Seven Stones as 'Region no. 5'. The continuation of these Tables is presented here as Table 1. The monthly mean for three periods are presented in Table 2.

TABLE 2. LONG-TERM MEANS FOR TEMPERATURE AND SALINITY AT THE SURFACE AT SEVEN STONES LIGHT VESSEL (50° 03′ N., 6° 05′ W.)

	Temperature (°C)			Salinity (‰)		
Month	1905–27	1928–39	1947–58	1904–27	1928–39	1947–58
January	9·95	10·14	10·46	35·261	35·275	35·241
February	9·38	9·55	9·59	35·256	35·291	35·241
March	9·18	9·33	9·47	35·248	35·272	35·242
April	9·55	9·85	9·93	35·245	35·278	35·242
May	10·81	11·11	11·11	35·225	35·270	35·245
June	12·92	13·62	13·33	35·227	35·253	35·219
July	14·90	15·37	15·28	35·213	35·245	35·171
August	15·75	16·22	16·19	35·179	35·207	35·105
September	14·61	15·41	15·50	35·191	35·203	35.118
October	13·28	13·66	13·99	35·238	35·248	35·183
November	11·87	12·33	12·63	35·261	35·264	35·270
December	10·84	11·05	11·51	35·264	35·265	35·255
Year	11·92	12·30	12·42	35·234	35·256	35·211

Changes in the long-term means are set out in Table 3. The warming up in the years 1928–39 was maintained during the years 1947–58 and indeed proceeded even further during the 8 winter months September–April. The Seven Stones region has much changed as a biological habitat since the first quarter of the century.

Salinity did not follow the same pattern. It increased during the period 1928–39 but has since shown a decrease. Such small changes in salinity, unlike those in temperature, are unlikely to have much effect on plants and animals.

Lumby's work covered the period up to 1927. In extending it for the Seven Stones Light Vessel up to 1958 we have adhered as closely as possible to his procedure. The statistical limitations and controls which he described at length apply here also.

TABLE 3. CHANGES IN LONG-TERM MEANS FOR TEMPERATURE AND SALINITY AT THE SURFACE AT SEVEN STONES LIGHT VESSEL (50° 03′ N., 6° 05′ W.)

	Temperature (°C)			Salinity (‰)		
Month	1928–39 less 1905–27	1947–58 less 1928–39	1947–58 less 1905–27	1928–39 less 1904–27	1947–58 less 1928–39	1947–58 less 1904–27
January	+0·19	+0·32	+0·51	+0·014	−0·034	−0·020
February	+0·17	+0·04	+0·21	+0·035	−0·050	−0·015
March	+0·15	+0·14	+0·29	+0·024	−0·030	−0·006
April	+0·30	+0·08	+0·38	+0·033	−0·036	−0·003
May	+0·30	Nil	+0·30	+0·045	−0·025	−0·020
June	+0·70	−0·29	+0·41	+0·026	−0·034	−0·008
July	+0·47	−0·09	+0·38	+0·032	−0·074	−0·042
August	+0·47	−0·03	+0·44	+0·028	−0·102	−0·074
September	+0·80	+0·09	+0·89	+0·012	−0·085	−0·073
October	+0·38	+0·33	+0·71	+0·010	−0·065	−0·055
November	+0·46	+0·30	+0·76	+0·003	+0·006	+0·009
December	+0·21	+0·46	+0·67	+0·001	−0·010	−0·009
Year	+0·38	+0·11	+0·50	+0·022	−0·045	−0·023

Observations in January–March 1950

Throughout 1949 very warm water had been present at the Seven Stones, the maximum deviation from Lumby's monthly means for the years 1905–27, +2·32° C, occurring in October. The whole of 1950 was there to remain warm but less so than 1949 (Table 1, Fig. 2). There may be an oscillation of temperature of approximately fortnightly period, the maximum tending to occur about the day before the new or full moon and the minimum about 5 days afterwards. A statistically sound result requires that data for a considerable number of years shall be examined. Until that is done any attempt to correlate in detail with some of the findings of Cooper, Lawford & Veley (1960) would be forced.

Throughout January water 0·13‰ less saline than average (i.e. water from the northern sectors) was followed by a sudden rise of 0·12‰ between 29 January and 1 February (Fig. 2). This betokened the first arrival at the Seven Stones of a water earlier observed to the southward. The winter minimum temperature of 10·0° C persisted with variations of no more than 0·1° C from 10 February to 15 March while salinity remained high (35·2‰).

The line of surface observations no. 10 from Lands End to Ushant was presented in an earlier paper (Cooper, 1960*b*, Fig. 3). About 12 February there was a narrow current around Lands End, but not including the position of the Seven Stones Light Vessel, of low salinity, relatively cold water from Lyme Bay which had flowed westwards along the coasts of south Devon and Cornwall (Cooper, 1958).

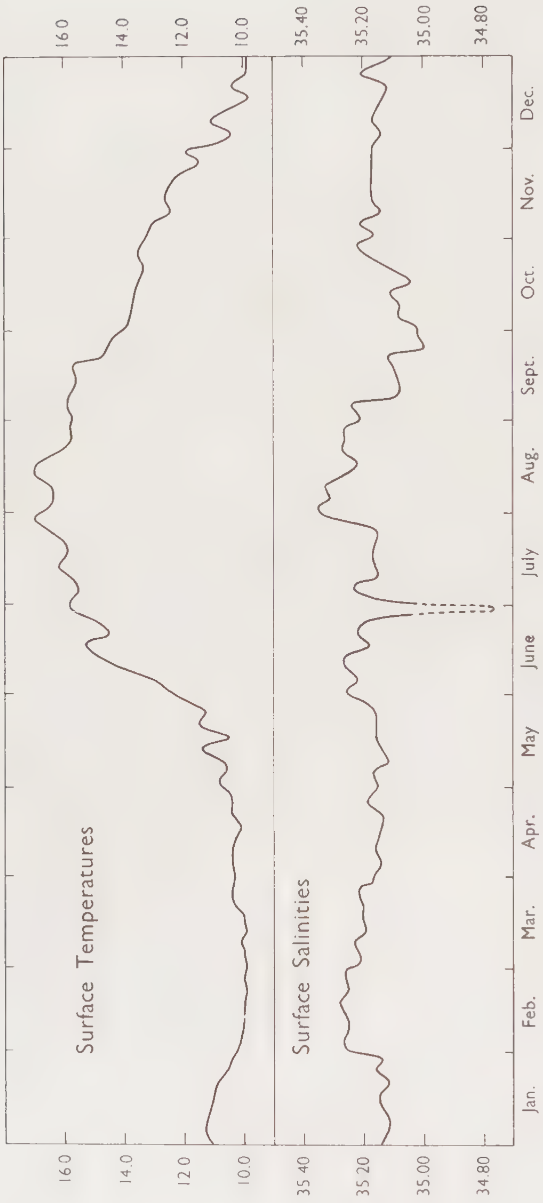

Fig. 2. Temperatures and salinities at the Seven Stones Light Vessel during 1950.

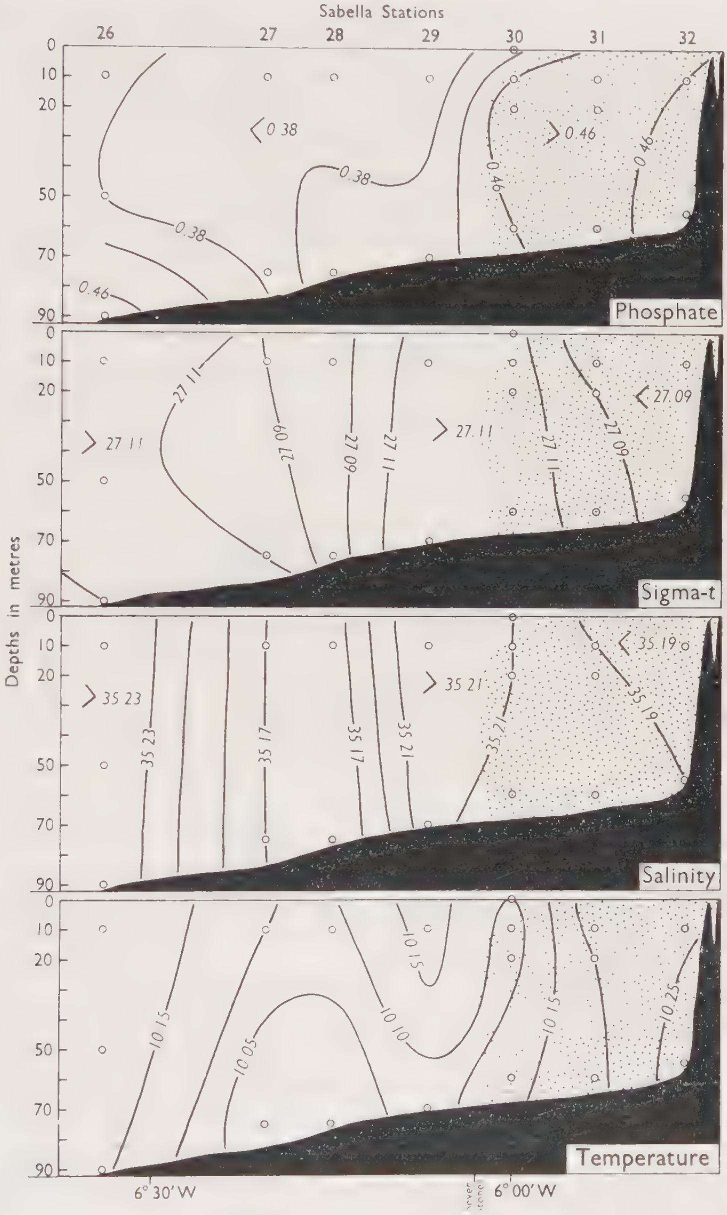

Fig. 3. Section across the Scilly–Lands End passage on 21 April for phosphate, the most informative measurement, for density and salinity, and for temperature which gave no useful information. The south Cornwall coastal water mass, revealed by phosphate, is shown stippled on each diagram.

Observations in April 1950

The cruise of R.V. 'Sabella' included a number of closely spaced Stations 26–32 in the Scilly–Lands End region (Fig. 3) on 21 April designed to elucidate the nature of the current around Lands End. In this they were indeterminate since, as we see now (Cooper *et al.* 1960), they were worked at spring tides when the gateway for the corner current from south to north of Cornwall may be closed. Full moon occurred on 17 April and the next new moon on 2 May.

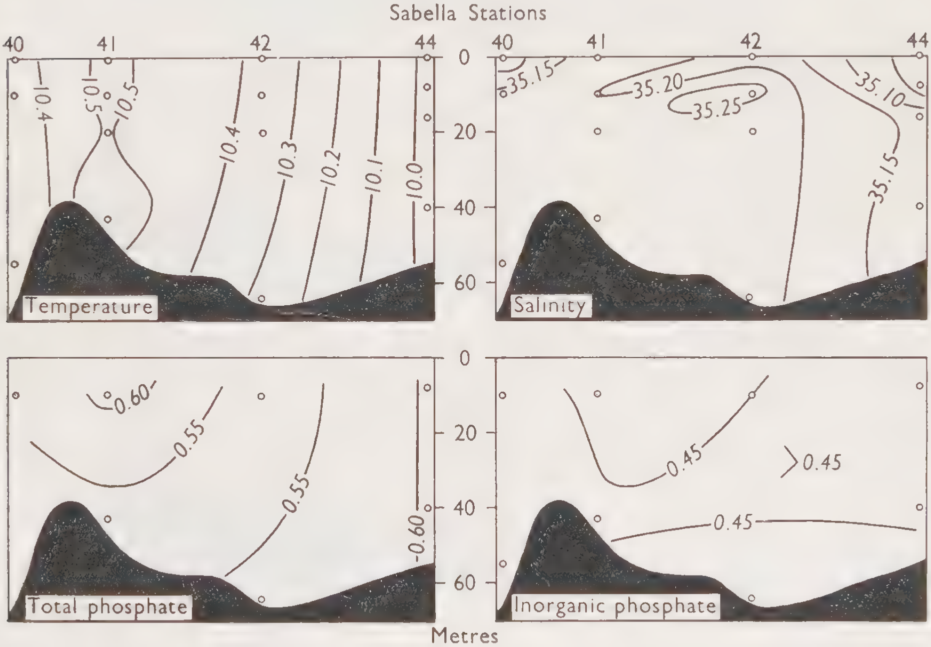

Fig. 4. Section off the north coast of Cornwall on 23–24 April to illustrate the homogeneous mass of water which can have come only from south of Cornwall. This water was markedly different from that to the north and west (sections not yet published).

The only firm evidence came from the phosphate analyses (Fig. 3) which clearly showed south Cornwall coastal water containing more than 0·46 μg-atom/l. P at Stations 30–32 and sharply differentiated from the poorer water to the westward. The boundary between the two lay to the east of the Seven Stones Light Vessel or under it at depths greater than 20 m. The south Cornwall coastal water is stippled in all four panels.

Although density and salinity records showed such small gradients, nevertheless, the boundary indicated by phosphate coincides with the belt of maximum density and salinity. Such a distribution of mass would come about from a weak counter-current towards the north around Lands End and another weak current towards the south-east running at the surface at the light vessel and at all depths to the westwards. Temperature distribution is not in conflict with such a current system but does not indicate it.

A line of stations off the north coast of Cornwall was run on 23 April (Fig. 4). Water with the properties of Stations 40, 41 and 42 was found nowhere else north of the fiftieth parallel, but its properties were closely similar to those of the waters south of Cornwall in the weeks before (Table 4). Whatever other evidence may suggest, there can be no doubt that there had been a flow of water from the south to the north coast of Cornwall. No such continuity is traceable in any other direction through the close net of stations (Fig. 1 in part). The deductions of Matthews and of Harvey are strongly supported.

TABLE 4. COMPARISON BETWEEN THE WATERS NORTH, WEST AND SOUTH OF CORNWALL, APRIL, 1950

Region ...	South Cornwall				
Ship ...	'Sula'	Interpolated in time	'Sir Lancelot'	'Sabella'	
Station	E 1	E 1	61	9	10
Date	23. iii.	21. iv.	8. iv.	18. iv.	18. iv.
Latitude °N.	50° 02′	50° 02′	49° 51′	49° 30′	49° 32′
Longitude °W.	4° 22′	4° 22′	4° 00′	5° 00′	5° 28′
Temperature °C	10·15	10·31	10·35	10·43	10·50
Salinity ‰	35·30–35·35	35·20	35·29	35·39	35·35
Density σ_t	27·10–27·20	27·08	27·20	27·20	27·16
Total phosphorus μg-atom/l.	0·53–0·55	0·53	—	0·69	0·63
Phosphate-phosphorus μg-atom/l.	0·43–0·49	—	—	0·40	0·44
Organic phosphorus μg-atom/l.	0·05–0·11	—	—	0·29	0·19
Region ...	Off Lands End			North Cornwall	
Ship ...	'Sabella'			'Sabella'	
Station	31	40	90	41	42
Date	21. iv.	23. iv.	30. iv.	23. iv.	23. iv.
Latitude °N.	50° 04′	50° 08′	50° 02′	50° 20′	50° 42′
Longitude °W.	5° 53′	5° 53′	5° 51′	5° 37′	5° 20′
Temperature °C	10·20	10·33	10·44	10·52	10·35
Salinity ‰	35·20	35·24	35·26	35·22	35·22
Density σ_t	27·10	27·10	27·09	27·05	27·10
Total phosphorus μg-atom/l.	—	0·57	0·56	0·57	0·54
Phosphate-phosphorus μg-atom/l.	0·49	0·47	0·41	0·44	0·43
Organic phosphorus μg-atom/l.	—	0·10	0·15	0·13	0·11

The Seven Stones current measurements held within themselves the probable answer (Cooper *et al.* 1960). The eastern half of the Lands End–Scilly passage may open and close to the passage of water from the south coast of Cornwall to the north like a trap door. It may open when the current at the light vessel sets to the south of its mean direction, an event favoured by neap tides and warm or very wet weather, and close when the current sets to the north of its mean position, an event favoured by spring tides and cold weather.

As we now reconstruct the occasion, water from off the south coast of

Cornwall including the position of station E1 and an interpolated position around 49° 45′ N. lat., 4° 40′ W. long. was being carried north-west as a counter-current towards the Runnelstone and Lands End. In this region mixing both horizontal and vertical was probably greatest at the time of springs while net northerly transport took place at neaps.

For an understanding of the oceanography of the Bristol Channel the sea area within 10 miles of the Lands End promontory is of much importance and deserves much more study than we have been able to give it.

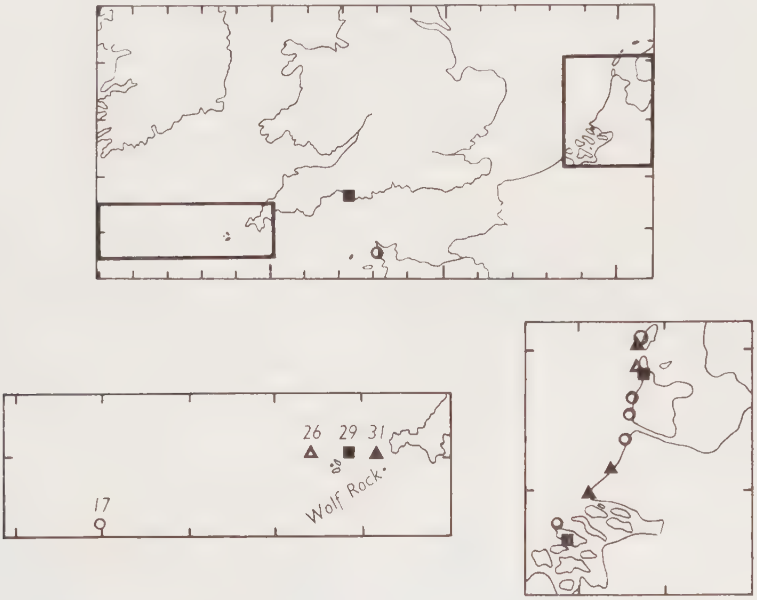

Fig. 5. Direction of surface drift. Four sets of bottles put out on 20–21 April at the positions shown by station numbers in the left inset. All recoveries are shown, most being along the Dutch coast as in the right inset.

Drift-bottle results

Four sets of surface drift bottles, provided by Mr David Vaux of the Lowestoft Laboratory, were put out from R.V. 'Sabella' during the April cruise west of Lands End. The bottles were fitted with 1 m drags of galvanized steel; the metal caps were sealed with pitch and painted white or red. The recoveries reported by Mr Vaux by letter on 29 April 1952 are of much interest (Fig. 5). To facilitate comparison with Carruthers's (1927) work, his position code is included.

At Station 17 (49° 28′ N., 9° 01′ W.) on 20 April 1950 at 00.25 h G.M.T. fifteen bottles were put out, of which six were recovered. Of these one travelled to Cap de la Hague (C55g), 282 miles at a rate of 1·9 miles/day. The other five grounded on the coast of Holland (J2f, J3b, J5j, J4h, J4h; 511–585 miles) at rates between 2·4 and 3·1 miles per day. Nine bottles were not recovered.

At Station 26 (50° 04′ N., 6° 34′ W., 10 miles N.W. of the Scillies), of five bottles put out on 20 April at 23.50 h G.M.T. only one was recovered near den Helder, Holland (J4c), after a journey of 476 miles at 3·1 miles/day. Four bottles were not recovered.

At station 29 (50° 04′ N., 06° 07′ W., north of the Seven Stones Light Vessel) of five bottles put out on 21 April at 03·20 h G.M.T., one was recovered a few miles east of Bridport, Dorset (B51d) after a minimum journey of 134 miles at a mean speed of only 1·1 miles per day. It is possible that this bottle, like the slow traveller stranded near Cap de la Hague, had travelled a roundabout route. Two more stranded in Holland in the mouth of the Schelde (H2j; 395 miles at 2·8 miles/day). Two bottles were not recovered.

At Station 31 (50° 04′ N., 05° 53′ W., 6 miles west of Lands End and where the corner current is believed to run) five bottles were put out on 21 April at 06.15 h G.M.T., 1½ h before high water Devonport. The tables of tidal streams (positions *E* and *F*) on Admiralty Chart no. 2565 (edition published on 5 August 1955) would suggest the tide would have been making at that time about 0·9 knots towards 40°, but was turning rapidly towards south to reach a maximum of 2 knots towards 195°. The set of the tide was thus such as to carry the bottles well south of the Wolf Rock into the fairway of the English Channel before it turned.

Three bottles were recovered on the coast of Holland between Hook of Holland and Texel (J3g; J2a; J5j) after journeys of 402–458 miles at 2·1, 2·4 and 2·5 miles per day. Two bottles were not recovered.

To sum up, from the thirty bottles put out at four positions in the Celtic Sea, eleven stranded on the coast of Holland, and one each on the mid-Channel coasts of England and France. These had drifted up-Channel with a mean speed of 2·6 miles per day. A surface skin of water had taken about 4 months to pass from end to end of the Channel. No bottles were anywhere recovered to suggest a northerly movement of surface water anywhere in the Celtic Sea. They are completely concordant with Carruthers's (1927) findings and with the pattern of currents which Carruthers *et al.* (1951) drew from their measurements at the Seven Stones Light Vessel.

The remarkably high values for compounds of phosphorus in bottom water at Station 25 on April 20 (Table 5, Fig. 1), and also at Station 26 can have arisen only by regeneration from the muddy deposits around the Labadie Bank or south of Ireland, as at Station 81. Thus west of the Scillies the bottom water was moving in a direction not very different from that shown by the surface drift bottles.

The drift-bottle measurements are also in accord with Russell's (1935) deductions from biological indicators that recruitment into the English Channel

TABLE 5. PROPERTIES OF BOTTOM WATER MOVING SOUTH-SOUTH-EAST TOWARDS THE SCILLY ISLES, 20–29 APRIL 1950

Station no.	Lat. (N.)	Long. (W.)	Depth (m.)	Temperature		Salinity (‰)	Density σ_t	Phosphorus µg-atom/l.		
				in situ (°C)	Corr. to 50° N. (°C)			Total	Inorganic	Organic
81	50° 45′	7° 30′	90	9·80	10·12	35·14	27·11	0·76	—	—
25	49° 58′	6° 56′	95	10·12	10·11	35·26	27·16	0·85	0·83	0·02

in April is of 'western' or 'elegans' type water. Moreover, the direction of flow was closely parallel with that deduced (Cooper, 1960*b*) from the Discovery II stations 100 miles to the southward a fortnight later, i.e. in the approach to the English Channel between 48° 20′ N. and 50° N. lat., the flow of water was everywhere easterly or somewhat south of east.

The drift-bottle results, particularly those from Station 31, combined with so much supporting evidence, are most unfavourable for one of the theses of this paper: that a corner current sets around Lands End from south to north.

The warm high salinity water found off north Cornwall on 23 April 1950 cannot be gainsaid. Any mechanism to get it there has to conflict with much other evidence. It seems inescapable that the current must flow with greatest strength either near the bottom or very close to Lands End, i.e. that it is intermittent and narrow and that the waters around the Longships Lighthouse need close attention.

Observations in June 1950

The 'Sabella' cruise in June 1950 was designed to find the origin and the fate of the nutrient rich water found west of the Scillies in April, to explore the waters lying inshore from the continental edge, to examine further the corner currents around Ushant and Lands End and the waters north and west of Cornwall and of Brittany and to obtain 'elegans' type water for Wilson's (1951) studies on differences between natural waters. The cruise was planned anti-clockwise but worked clockwise. Since the planned stations were not renumbered, we started with Station 34 (identical with E1) and finished with Station 1 (Fig. 1).

Stability and nutrient availability

Information as to potential productivity of different sea areas during the summer months emerges from a comparison of adjacent stations worked on the April and June cruises (Fig. 6, Table 6).

At position *P* well away from the nearest land and with a 1·0 knot spring tide, the temperature below 40 m. depth scarcely increased at all and a very strong thermocline developed (Fig. 7). The stability at positions *Q* and *R*, similarly placed, was nearly as great. Once the spring diatom outburst was

TABLE 6. POSITIONS WORKED IN APRIL AND JUNE 1950, STUDIED FOR STABILITY AND POTENTIAL PRODUCTIVITY

Mean position	Mean lat. (N.)	Mean long. (W.)	Distance of stations apart (miles)	April cruise		June cruise		Rate of tidal streams at springs, knots
				Date	Station no.	Date	Station no.	
P	50° 04′	7° 29′	8	20	24	14	15	1·0
Q	49° 32′	7° 30′	4	19	14	14	17	0·7
R	50° 39′	5° 28′	4	30	88	15	11	1·2
S	49° 29′	4° 51′	12	18	9	13	32	1·5
T	50° 04′	5° 47′	0	21–30	31, 32, 40, 90	16	4	Strong
U	50° 21′	5° 37′	2	23	41	15	5	1·4
V	50° 41′	5° 20′	3	23	42	15	6	1·4

TABLE 7. CONSUMPTION OF PHOSPHORUS COMPOUNDS AT POSITIONS *R–V* (μg-atom/l.)

For development of thermocline structure compare Fig. 7.

Sea area	Depth (m)	Total phosphorus		Inorganic phosphate	
		Consumed since April	Remaining on 13–16 June	Consumed since April	Remaining on 13–16 June
Celtic Sea away from coast, position *R*	10	0·28	0·32	0·26	0·14
	20	0·28	0·31	—	—
	40	0·02	0·54	—	—
	70	Nil	0·57	−0·05	0·49
	88	Nil	0·59	—	—
Entrance to English Channel, position *S*	0·5	0·25	0·46	0·24	0·18
	10	0·21	0·50	0·25	0·19
	20	0·17	0·54	0·14	0·25
	50	0·17	0·55	0·09	0·30
	70	0·26	0·42	0·06	0·31
	90	0·19	0·46	0·03	0·32
In Lands End corner current, position *T*	10	0·13	0·37	0·27	0·18
	48	0·20	0·30	0·27	0·18
North-north-east of Lands End, position *U*	10	0·29	0·32	0·24	0·18
	20	0·26	0·31	0·27	0·17
	43	0·19	0·34	0·30	0·16
Position *V*	0·5	0·16	0·36	—	—
	10	0·19	0·33	0·31	0·14
	20	0·21	0·32	0·25	0·19
	30	0·23	0·31	—	—
	61	0·25	0·31	0·21	0·20

over, there could have been little replenishment of the surface water by nutrients from below.

Only at position *R* have we data to illustrate this (Table 7). Below 40 m. where the water had warmed up only 0·3° C there had been no consumption of phosphate. Vertical stability had been sufficient to immobilize the reserves in the deeper water. Only the reserves remaining in the uppermost 20 m were available for plant production which must subsequently have been restricted. The tidal streams around positions *P* and *R* may exceed 1 knot so that we may conclude that such tides running over a bottom 100 m deep and well away from land are unable to hinder the rapid formation and maintenance of a strong thermocline in late spring and summer.

Earlier (Cooper, 1960*b*) it has been deduced for the area north of Brittany that once the thermocline has developed strongly, vertical exchange across it becomes trifling and temperature in the deeper waters becomes conservative. This conclusion evidently applies at position *P* and to a less degree at positions *Q* and *R*, even in late spring. Moreover, any movement there may have been there between 20 April and 15 June was essentially along a west–east axis.

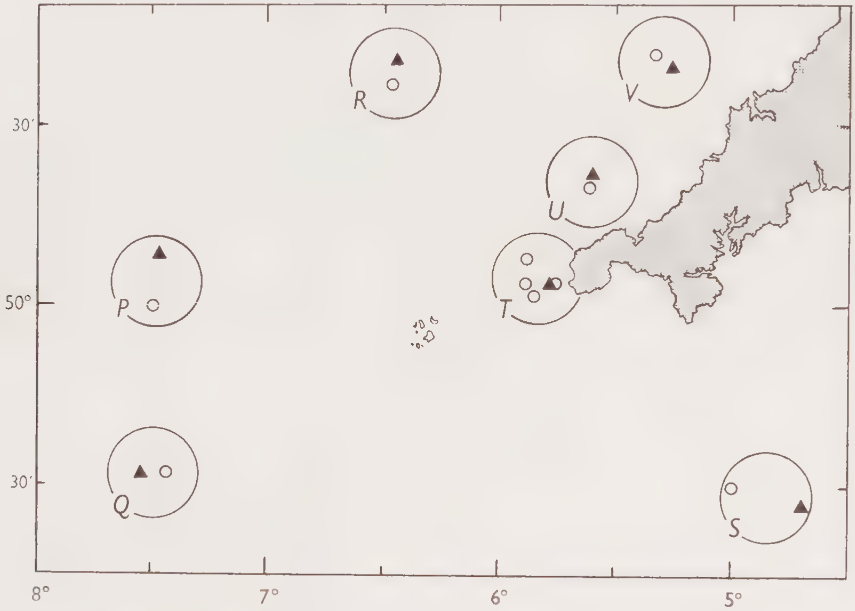

Fig. 6. Positions of stations used for the study of stability and potential productivity; open circles, April; triangles, June.

Position *S* (Fig. 7) was on the centre line of the mouth of the English Channel and spring tides there may reach a rate of 1·5 knots. Hereabouts the deeper water warmed up by 1·4 C and the surface layers only three-fifths as much as in the open Celtic Sea. Total phosphorus (about 0·2 μg-atom/l.) had been withdrawn from the whole water column into forms not sampled with the water. Inorganic phosphate had fallen by only 0·06 μg-atom/l., i.e. about 0·2 μg-atom/l. of phosphorus in organic combination had been regenerated in the deeper water.

Later in the summer it has been shown (Cooper, 1960*b*) that the deeper water around position *S* had warmed up by transport of water, with conservation of properties, from the level of the thermocline west of Ushant.

This movement from the south-west was quite definitely not occurring in May and June 1950. It is much more probable that in spring, in an area where strong tides (1·5 knots at springs) slow down the development of the thermocline, considerable vertical exchange by turbulence between the upper and lower layers may persist longer than where tides do not exceed 1 knot.

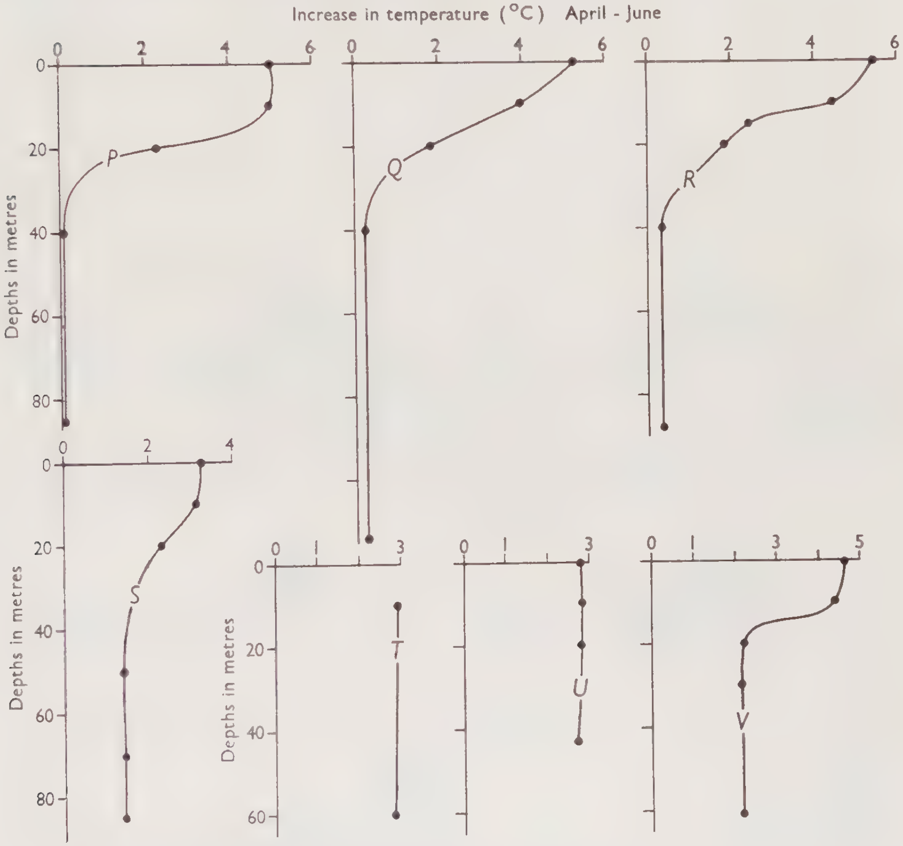

Fig. 7. Increase in temperature at seven positions (Table 6) in the Celtic Sea between 19–30 April and 13–16 June 1950.

Consequently in the mouth of the English Channel turbulent mixing somewhere or other, but not necessarily at the place of observation, is sufficient in spring before the thermocline is fully developed to carry considerable replenishment of phosphate from the deeper reserve to the illuminated upper layers. Moreover, some of this phosphate was passing through a second cycle of utilization. Around midsummer, but not later, the position *S* was likely to be more productive than positions *P*, *Q* and *R*.

The Lands End corner current

Position *T* (Figs. 6, 7, 4 (Station 40) and 8 (Station 4); Tables 6 and 7) was close to Lands End in the corner current in which vertical mixing remained almost complete. The water column in June was almost isothermal (13·05–13·15°), isohaline (35·16–35·19‰) and isopycnal (σ_t 26·50–26·55). Contents of total phosphorus and inorganic phosphate at Station 4 on 16 June and at the four stations (31, 32, 40 and 90) worked on 21, 23 and 30 April, cannot be reconciled since the consumption of inorganic phosphate considerably exceeded the consumption of total phosphorus. Sampling in the Lands End corner current, more than in most places, is snap sampling of a highly dynamic system. The water being mixed up in June was of quite different origin from that in April. A small but distinctive water mass is created in the Lands End corner current and its components differ according to the time of year, and probably at different times in the lunar month. Consequently, in the sea area north of Cornwall an assessment of biological productivity in terms of the difference between the winter maximum and the summer minimum of inorganic phosphate is unlikely to be worth while.

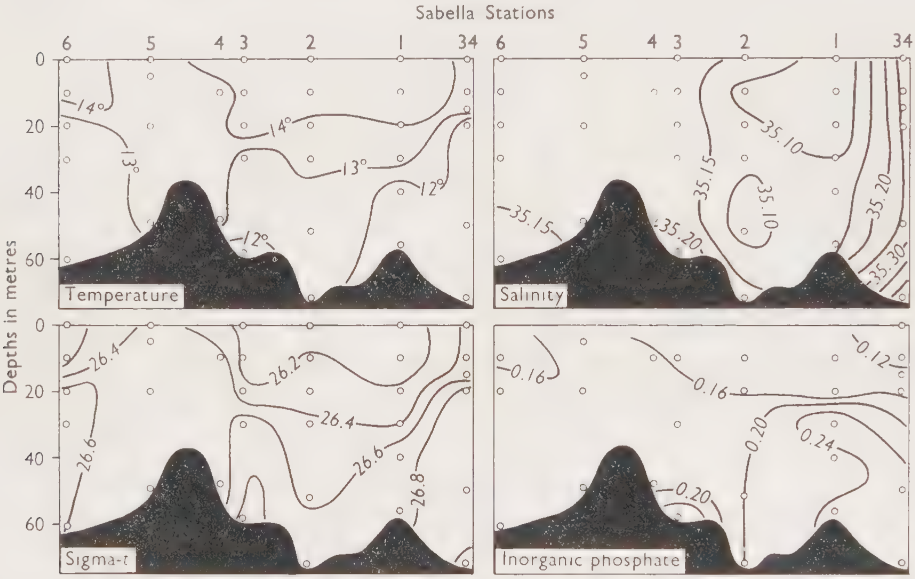

Fig. 8. A vertical section on 12–16 June along the line of travel of water from the south coast of Cornwall to the north (see Fig. 1 for positions). The strongly stratified water off the Runnelstone (Station 3) can be recognized off Lands End (Station 4) and north of St Ives (Station 5) except that it has been intensively mixed. At Station 6, a thermocline has started to reform.

The June cruise was laid out to decide whether the water lying close to

Lands End moves north or south. Station 3 was worked one mile south of the Runnelstone. It cannot have failed to sample water escaping to the south, if any there was. The water at Station 3 was as strongly stratified as any other in the northern English Channel (Stations 34–32, 2 and 1; Figs. 1, 8 and 9) and more strongly than most. The water at the Runnelstone was unexceptional English Channel water, probably contributing to the corner current but very definitely receiving nothing from it.

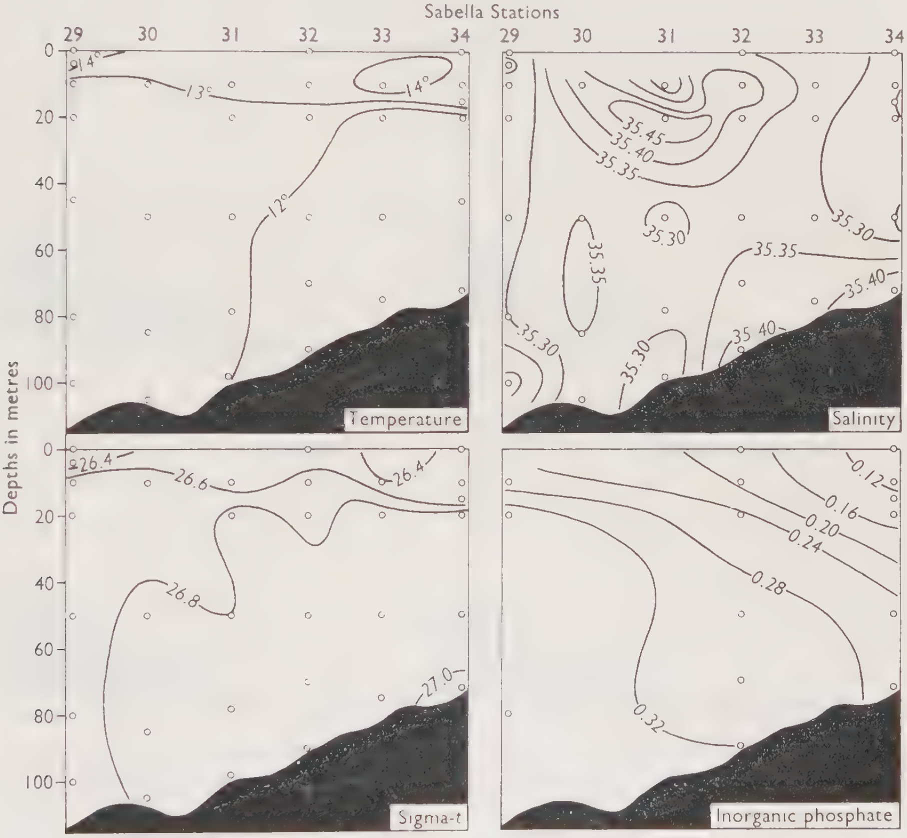

Fig. 9. A vertical section on 12–13 June from near Ushant (Station 29) to E 1 (here Station 34).

The north Cornwall water in June 1950

The Stations to the north (here grouped as positions *U* and *V*; Figs. 1, 6, 7, 8 and 10) present a very different story. At position *U* (incorporating June Station 5) the whole homogeneous water column was 2·8° warmer in June than in April. The tidal stream was no stronger than at Station *S*, or off the

Runnelstone. We had here the mixed water produced in the Lands End corner current. Its influence was still very marked at position *V* (incorporating June Station 6) 23 miles on.

The argument for June is quite different from that used in April but is equally convincing. Much of the North Cornwall water had arrived by way of a narrow current around Lands End. Russell's illustration (1936, fig. 6), based on the occurrence of biological indicators, of the water masses around Lands End in July 1935 is in quite remarkable agreement with this account derived entirely from physical and chemical observations.

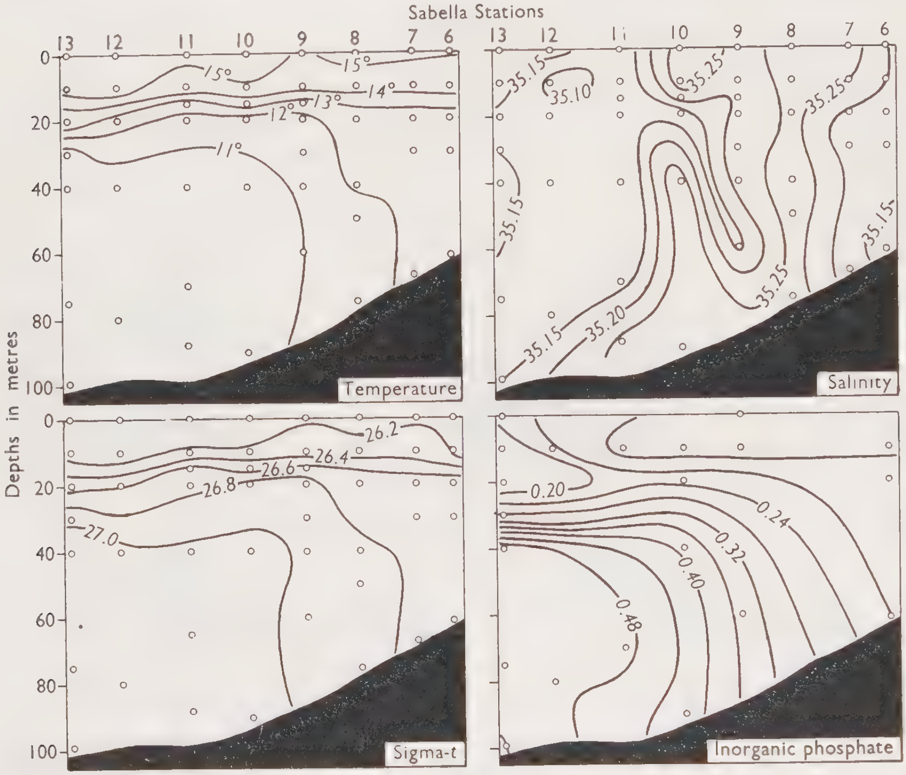

Fig. 10. A vertical section north of the Scillies along latitude 50° 41′ N. on 15 June. The doubts about the data where two currents adjoin at Stations 9 and 10 are discussed in the text.

An inflexion of geopotential (Figs. 10 and 11) at Station 10 represents clearly the western boundary of the warm and saline relatively well-mixed water emerging from the Lands End corner current (Stations 9–6) with the cold, less saline water of the Northern Celtic Sea (Stations 13–11). The June Stations 9 and 10 contain anomalous salinities, confirmed by the analyst, which it is quite impossible to contour according to accepted principles of oceanographic presentation. The contouring in Fig. 10 is the least improbable if no data are rejected. I have not attempted to reconcile T, S and σ_t between Stations 9 and 10 in this drawing. Either we must reject at least two duplicated analyses or we have to accept strong eddying at the current boundary with some accompanying instability, amounting to σ_t 0·06. Stations 9–6 and 5 (Figs. 8 and 10) represent a water mass in the southern entrance to the Bristol Channel with a history comparable with stations 31 and 30 (Fig. 9) in the southern entrance to the English Channel at the same time (Cooper, 1960*b*). Both had been reformed around headlands. In June 1950, considered as a model, the Bristol Channel was much easier to study.

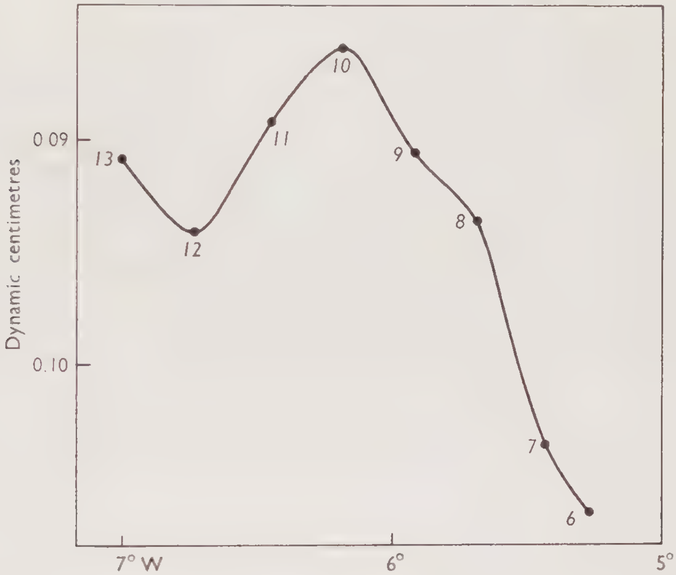

Fig. 11. Geopotential heights along latitude 50° 41′ N. (Stations 13–6 on 15 June); surface compared with 70 m.

The concept of narrow well-mixed corner currents running at depth round headlands and then fanning out under the influence of their momentum and the earth's rotation is a fruitful one from both a physical and biological point of view. It requires more proof than is given here, since cruises such as ours in 1950 were wrongly conceived. An understanding of corner currents requires intensive studies using a variety of techniques and spread over at least a fortnight.

Biological consequences of the Lands End corner current

Some biological consequences may also be deduced for both shore and planktonic flora and fauna of north Cornwall between Cape Cornwall and Hartland Point.

Under winter isothermal conditions

The Lands End corner current may incorporate three types of water, (i) south Cornwall coastal water containing run-off from the rivers of south Cornwall and south Devon, (ii) water from the western approaches south of Scilly, and (iii) water from north of Scilly which the current measurements of Carruthers *et al.* (1951) suggest often passes the Seven Stones Light Vessel proceeding south-east. Since mixed waters are often productive there may be a tendency, but in winter no more than a tendency, for the waters north of Cornwall to be somewhat more productive than those to the west and south.

In summer when thermoclines may form

The three geographical areas specified for winter should contribute in summer also but each may contribute three types of water, one from above, one from below the thermocline and another from within the thermocline containing detritus in course of regeneration. The upper waters may be stripped of nutrients and both upper and deeper waters may contain organic substances resulting from the metabolism of the plants and animals that have lived in the water and in the muds of the Labadie Area. The mixing pot provided by the Lands End corner current in summer is likely therefore to create a water which may mature as a productive, possibly highly productive, water off the north Cornwall coast. It may well be able to develop characteristic indicator species. Not only the plankton but the shore flora and fauna may reflect this in the months June–September.

This argument also suggests that animals living permanently at a depth greater than 30 m. north of Cornwall will find warmer conditions between July and September than those so living south of Cornwall. Consequently a comparative study of bottom fauna north of Cornwall may find, in those species which are controlled by summer temperatures, resemblances with the fauna north of Brittany rather than south of Cornwall. Setting off the two-degree difference in latitude against the secular rise in temperature in this region, comparison may prove closest between the north Cornwall bottom fauna of today with the north Brittany bottom fauna half a century or so ago.

The Bristol Channel as a site for experiment

The Bristol Channel offers a better site for experimental studies than the English Channel, because there is no eastern exit corresponding to the Straits of Dover, because it receives the largest river in England and Wales and much sewage and industrial waste, because the contrast in salinity and temperature on the north and south sides is usually greater than in the English Channel, and because the area requiring study is smaller.

A meteorological consequence of the Lands End corner current

West Cornwall, a narrow peninsula, is well known for differences in weather between its two coasts, the north coast in popular repute being the more bracing. Between 1 and 5 August 1945 I was engaged in a co-operative investigation involving boats working from Falmouth (Fig. 1) and aircraft based on Portreath. On the south coast the weather was superb throughout whereas the north was blanketed with fog. This fog was entered at the crest of the road between, while the aircraft had regularly to use Predannack, only 18 miles from Portreath but on the south coast, as an emergency base.

This very strong contrast evidently reflects differences in air and in sea temperatures on the two coasts. An intermittent corner current bringing variable amounts of well-mixed relatively saline water round to the north coast to replace Bristol Channel water is likely to control these local variations in weather.

The northern side of the Bristol Channel has a much more estuarine character than the northern side of the English Channel west of Start Point. The southern side of the Bristol Channel may be bathed in turn by either kind of water or by water from west of the Scillies or by mixtures of these. Waters from the south will also be subjected to vertical mixing whilst in the corner current. It is clear that an understanding of the local climate of north Cornwall, especially of fog formation, may be had only if the behaviour of the Lands End corner current is more fully understood.

I wish to acknowledge the cordial co-operation of Captain C. A. Hoodless then master of R.V. 'Sabella' and his crew, also of Mr P. G. Corbin, Mr G. A. Robinson and Mr G. R. Forster on the cruises in April and of Mr A. D. Mattacola on that in June. The salinities were determined by the Government Chemist and inorganic and total phosphorus by Mr F. A. J. Armstrong. I am also much indebted to the Lowestoft Laboratory for their assistance during the joint 1950 programme, in particular to Mr David Vaux who discussed many of the issues at the time and provided the clear-cut drift-bottle data. These have very severely restricted the possibilities that could be considered and in the end have given more confidence to the solution now presented. The paper has been illustrated by Mr G. A. Battin.

SUMMARY

Measurements of currents by meters and drift-bottles, of temperature, of salinity and of phosphate at the Seven Stones Light Vessel and in the encircling waters around Lands End and the Scilly Isles have led to conflicting conclusions on water movement. The conflict may be resolved if it is assumed that a narrow well-mixed corner current flows intermittently around Lands End

from the south to the north coast of Cornwall. Evidence obtained in 1950 is produced in support of this deduction and supported by a development of the current measurements at the light vessel in an accompanying paper with Lawford and Veley.

It is suggested that the Lands End corner current may create conditions north of Cornwall to encourage development in summer of a small but characteristic biological community on the shore and on the off-lying sea bed and to create a local climate rather different from that off the south coast.

The Bristol Channel is considered to offer a better site for experimental oceanography than the English Channel.

Information on the effect of tidal streaming on biological productivity in summer is presented.

Temperature of the water at the Seven Stones Light Vessel has increased on average by about 0·3° C in the spring months and by about 0·7° C in autumn.

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ON VARIATIONS IN THE CURRENT AT THE SEVEN STONES LIGHT VESSEL

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(Text-figs. 1–4)

Measurements of current at the Seven Stones Light Vessel, 50° 03·5′ N. lat., 6° 05·1′ W. long. (for position, see Cooper, 1960*b*, fig. 1) were first made with the Carruthers Drift Indicator between 17 August and 15 September 1933 (Carruthers, 1934). The much longer series with the Vertical Log between July 1939 and April 1941 showed average travel of the residual current at a rate of 2·5 miles per day towards east-south-east (110° true) (Carruthers, Lawford & Veley, 1951). It was shown clearly that there was a strong causal connexion between the direction and strength of the wind and direction and strength of current, but that there were evidently other factors concerned as well. These current measurements were not easy to reconcile with deductions from the observed distributions of temperature and salinity in the area (Matthews, 1914; Harvey, 1925, 1929; Cooper, 1960*b*). A rational explanation could be achieved if it is assumed that the passage of water from the English Channel to the Bristol Channel occurs intermittently and is confined to a narrow current close into Lands End. This 'corner current' rarely extends as far west as the Seven Stones Light Vessel.

During 1950 as a result of R.V. 'Sabella's' work on 20–24 April 1950 we deduced from a study of the observed winds the probable current at the Seven Stones for the 3 days when R.V. 'Sabella' was in the vicinity (Table 1). Around 21–23 April the predicted residual current was, no doubt, setting towards 120 . This is close to the direction 110 (true) computed for the average water movement over the whole period of 600 days in 1939–41. On 21 April 'Sabella' Stations 30 and 29 bracketed the position of the light vessel and Stations 27 and 28 were 8 and 12 miles to the westward and immediately north of the Scilly Islands; they were occupied by water of relatively low temperature and salinity. This is a consistent picture of a movement of water

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TABLE 1. PREDICTED RESIDUAL WATER MOVEMENTS AT SEVEN STONES LIGHT VESSEL

Date, April 1950 ...	21		23		30	
	Speed m.p.d.	Dir.	Speed m.p.d.	Dir.	Speed m.p.d.	Dir.
Intrinsic water movement irrespective of tides	2	50°	1·5	10°	3	100°
Water movement produced by winds	4·1	155°	4·3	145°	6·4	15°
Residual water movement	4	125°	3·5	120°	7·5	40°

from the north-west. The water at Stations 27 and 28 had much in common with that at Station 89, 14 miles to the north on 30 April. This distribution is also consistent with the eastern sector of an eddy or rising centre conditioned by the distribution of density during a period of warming up within and around Scilly (Cooper, 1960*a*).

Again (Cooper, 1960*b*) the distribution of temperature and salinity west and north of Cornwall in April 1950 (Cooper, 1960*a*, fig. 4) could be understood only if a very considerable transport of water had occurred during the preceding neap tides but had been suppressed by the spring tides occurring when the observations were made. Also in the observations of temperature and salinity at the Seven Stones in 1950 (Cooper, 1960*b*, fig. 2) there is a suggestion of lunar periodicity in summer.

We therefore further analysed the 1939–41 current observations for the effect of tide and season. There are three restrictions inherent in the analysis. (i) The current is much influenced by wind and by factors at a distance from the Seven Stones. Over the whole period, the strength of the mean residual local wind was only 3% of the maximum strength recorded. But when individual lunar months are considered, the strength of the mean residual local wind may be as much as 30% of the maximum and cannot then be neglected. (ii) The vertical log current meter used reads the direction of water movement only to within ±22½°. Summing and averaging may considerably reduce the error of the mean measurements. (iii) In these computations, the *magnitude* and *direction* of the residual water movement were treated independently, i.e. the directions (or magnitudes) were 'summed' algebraically and divided by the number of days involved.

The first step in the analysis was to determine the mean direction of the residual water movement during each of 22 consecutive lunar months (Fig. 1, lower). The direction varied between 90° and 150°, the mean for the whole period being 114°.

The variation in direction of the residual water movement about its over-all mean seems to be periodic, being to the north of the mean in winter and spring and to the south during summer and early autumn. Most of the 'peaks' on the plot coincide with periods when the residual wind was either very strong or blew from directions at right angles to the mean direction of the residual water movement. Taking this into account, it is suggested that the intrinsic residual water movement is most northerly in December and most southerly in July.

The variation in flow (magnitude) of the residual water movement per lunar month (Fig. 1, upper) is not as clear as the variation in direction. However we suspect that at the time a long-term periodic factor was decaying, so that the plot of mean values should be read about the pecked line tentatively drawn in. It would seem that the mean magnitude of the residual water movement may be higher in winter and spring and lower in summer and autumn.

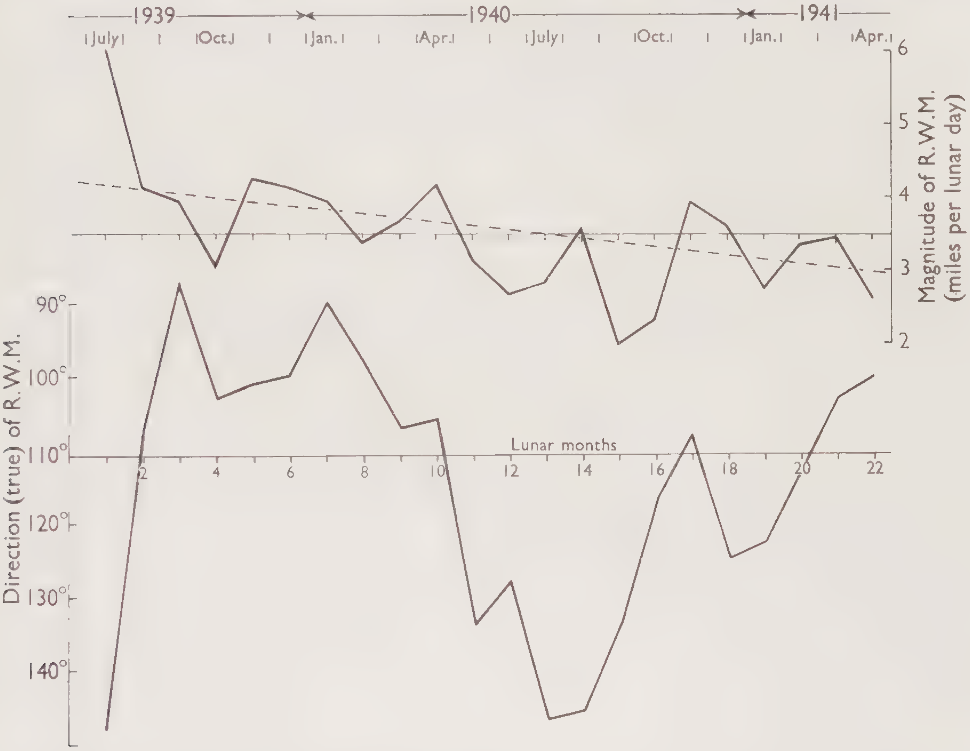

Fig. 1. Residual water movements at the Seven Stones Light Vessel during individual lunar months between July 1939 and April 1941. Upper panel, magnitude in miles per lunar day; lower panel, true direction.

The high magnitude for the residual water movement in July 1939 provides a problem; however, the mean wind during the lunar month favoured this residual water movement and may have accounted for about 2 miles per day of the 6 miles per day found.

The direction of the current is not closely tied to either sea or air temperatures. For this comparison calendar months are more convenient (Fig. 2). It is most unfortunate that due to war conditions the temperature records were maintained only for the first 4 months of the Vertical Log measurements so that a direct comparison between sea temperature and current direction cannot be made. A comparison is here made between the monthly mean temperature over the years 1928–39 (Cooper, 1960*b*, table 1) and the monthly mean residual current.

It will be seen that changes in sea temperature follow changes in current direction with a considerable time lag. The association is better between current direction and air temperature at Scilly, particularly in 1941, but one would hesitate to say that such association is at all close.

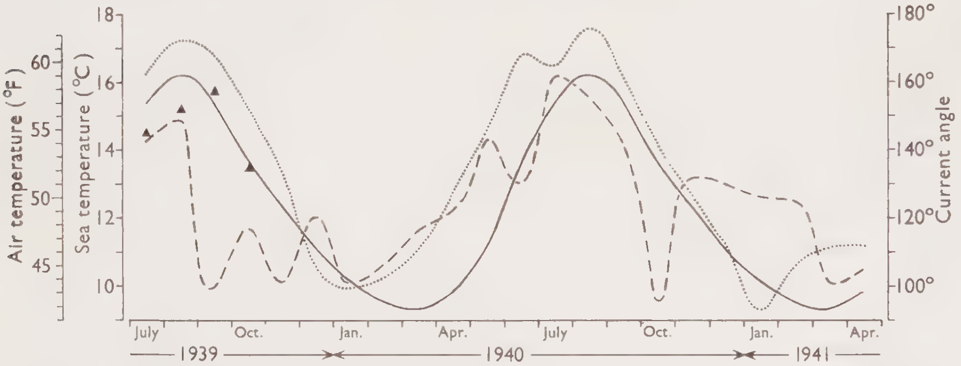

Fig. 2. Comparison between the mean direction of the current (pecked line) during the individual calendar months July 1939–April 1941, with the mean monthly sea temperatures (full line) at the light vessel for the years 1928–39 and the mean monthly air temperatures (dotted line) at St Mary, Scilly, during the same months as the current observations. Black triangles denote the four monthly sea temperatures observed at the light vessel at the start of the current measurements.

From the results of the 1950 cruises it had been deduced that the corner current may run most strongly around Lands End at neaps and be held back at springs. Consequently for each lunar month of the 1939–41 measurements we calculated the daily deviations from the mean direction of the water movement appropriate for that month. From these for each day of the generalized lunar month an average deviation of the direction of the residual water movement, clockwise or anti-clockwise, was obtained (Fig. 3, lower).

These deviations (maximum 27) were of the same order as the error of single measurements. Nevertheless, it is reasonably certain that the residual water movement deviates to the northward of the mean in the vicinity of the springs and to the southward in the vicinity of the neaps. The deviation is greater at neaps than at springs but occurs for a shorter period. There are marked 'reactionary' deviations on either side of new moon, however, and

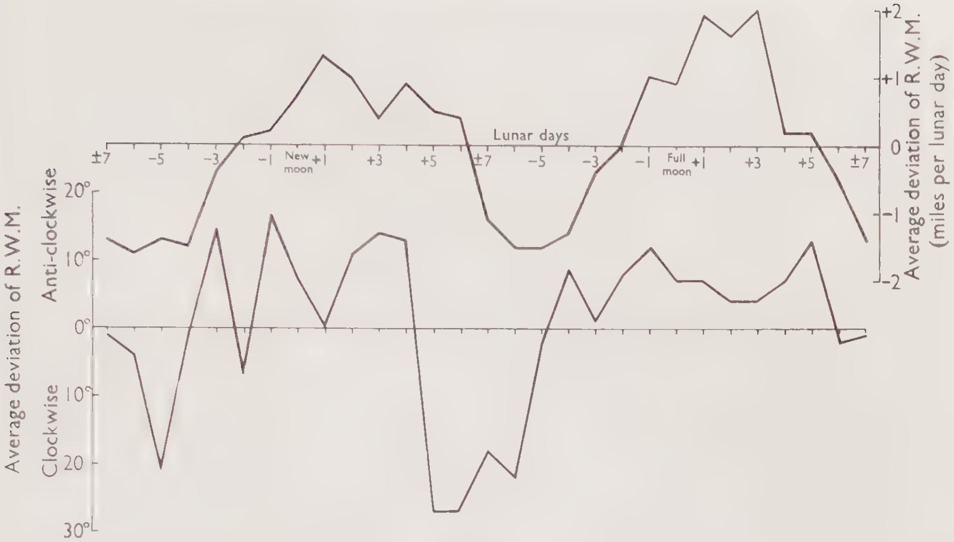

Fig. 3. The average deviation of the residual water movement from the mean for each lunation (lunar month) drawn for each day of the generalized lunation. Upper panel, magnitude in miles per lunar day; lower panel, direction.

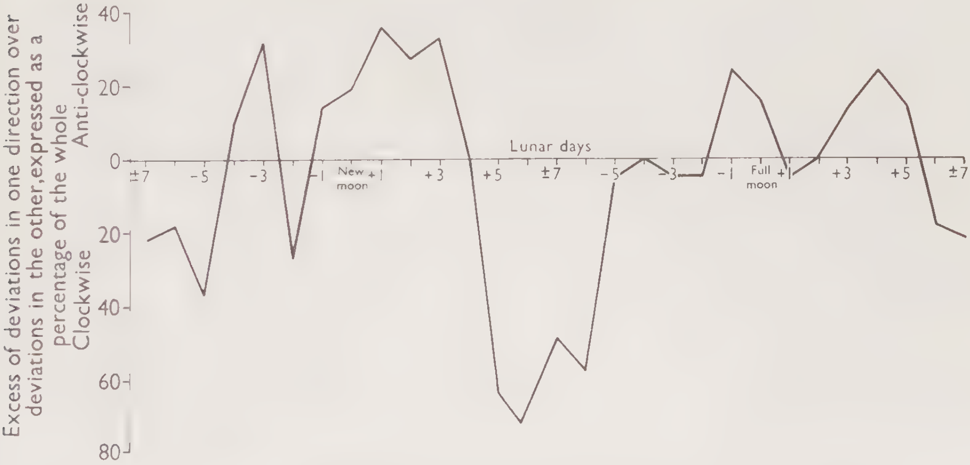

Fig. 4. Frequency of deviations of the residual water movement from the mean for each day of the lunar month.

less marked ones on either side of full moon. It is just possible that this may be due to the wind, on the majority of days involved, being unfavourable to the intrinsic direction of the residual water movements but, as the plot is for a mean of 22 lunar months it is more likely that there is in fact some reaction towards the opposite side of the mean direction for the month.

The plot of the daily deviations from the mean magnitude of the water movement appropriate for each lunation is satisfactory (Fig. 3, upper) with high residuals at springs and low ones at neaps. This curve illustrates the point made earlier (Carruthers *et al.*, 1951) that there are split maxima at springs and a well-defined minimum at neaps.

For any particular day of the lunar month the chances that the direction of the residual water movement would deviate clockwise or anti-clockwise from the mean of the month are plotted in Fig. 4. The percentage on each day of the lunar month was obtained by subtracting the number of times the residual water movement deviated in one direction from the number of times it deviated in the other and dividing by the sum of the two. Occasions when the residual water movement did not deviate from the mean were counted as $\frac{1}{2}$ to each direction.

There is a marked resemblance between Figs. 3 (lower) and 4. The latter confirms the 'reactionary' deviation (more southerly residual water movement) at New Moon minus 2 but not at New Moon plus 1. It confirms the 'reactionary' tendency at Full Moon minus 3 and enhances it at Full Moon plus 1 and plus 2.

DISCUSSION

There is strong evidence that at the Seven Stones Light Vessel the residual current tends to deviate to the south of the mean direction at neap tides and in summer and to the north of the mean direction at spring tides and in winter.

In April 1950 serial observations at the time of the spring tides failed to produce conclusive evidence of a considerable corner current around Lands End, but the distribution of temperature, salinity and nutrients north of Cornwall (Cooper, 1960*a*, fig. 4, and 1960*b*) left no doubt that there must have been such a corner current very shortly before, probably at the time of the preceding neaps.

It seems reasonable to infer that the Lands End corner current is favoured by (1) presence along the south coast of Cornwall of light water produced by heating during warm weather or by dilution at any time of year by run-off after heavy rainfall over south-western England, (2) a tendency to an anticyclonic eddy around the Scilly Island group during warm weather, (3) a current direction at the Seven Stones Light Vessel setting well to the south of the Runnelstone, (4) weak currents at the light vessel, (5) neap tides (i.e. that the Lands End corner current will be most evident during neap tides in very warm or very wet weather).

Conversely, the Lands End corner current may be hindered by (1) homogeneous water stretching south of Cornwall, as after a heavy south-westerly gale, (2) a tendency to a cyclonic eddy around the Scilly Island group during cold weather, (3) a current at the Seven Stones lightvessel setting east towards the Lands End promontory, (4) spring tides, though these may mix waters ready to be carried around on the following neap tides.

Our argument has included neither what may happen when the current at the lightvessel sets towards a northerly or westerly direction, nor what may happen during severe gales which may override the forces acting during moderate winds.

SUMMARY

On a first appreciation, findings during the cruise of the Plymouth research vessel 'Sabella' around Lands End in April 1950 appeared to conflict with conclusions drawn from long-period measurements of current at the Seven Stones Light Vessel. The results could be harmonized if it is assumed that there may be a narrow intermittent current around Lands End, transporting water from the south to the north coast of Cornwall and rarely extending as far west as the Seven Stones Light Vessel.

A detailed examination gave strong support to this explanation but the desired direct confirmation has, unfortunately, not yet been attempted.

The conclusions are set out in the Discussion.

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THE INFLUENCE OF TEMPERATURE ON THE BREEDING AND THE MOULTING ACTIVITIES OF SOME WARM-WATER SPECIES OF OPERCULATE BARNACLES

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(Text-figs. 1 and 2)

Thorson (1946) considered in detail the earlier views of Appellöf (1912), Orton (1920) and Runnström (1928) that breeding activities of the majority of marine organisms were controlled by the temperature of the sea and referred to this as Orton's rule. Recently Crisp (1954) and Qasim (1956) also reviewed the existing literature on this subject in relation to barnacles and fish. By considering the seasonal availability of planktonic food in conjunction with Orton's rule, they explained why tropical species inhabiting cool temperate waters have a breeding season confined to the warmer months, whereas boreo-arctic species throughout their whole range breed only during colder months.

Loosanoff & Davis (1950) succeeded in bringing the bivalve mollusc *Venus mercenaria* into the spawning condition by gradually raising the water temperature and providing suitable food. Patel (1959) maintained specimens of *Lepas anatifera* L. under laboratory conditions, raised the temperature, and fed them on *Artemia* larvae and thereby induced the species to breed. On the other hand, Crisp (1957) reported moderate success in causing the breeding of certain boreo-arctic barnacles during the period when the natural population was not breeding by lowering the temperature.

It was considered desirable to have a liberal supply of fertilized egg masses, larvae and cyprids of the commoner fouling organisms, especially of cirripedes, at all the seasons of the year for conducting experimental work. The following experiments were carried out to induce these animals to breed outside the normal breeding period of the natural population. Simultaneously, consideration was given to the influence of temperature on moulting rhythm, cirral activity and egg size.

Tropical or subtropical species of operculate barnacles inhabiting British waters, namely *Chthamalus stellatus* (Poli), *Elminius modestus* Darwin, *Balanus perforatus* Bruguière and *B. amphitrite* var. *denticulata* (Broch), were selected for the investigation.

MATERIAL AND METHODS

Specimens of *Chthamalus stellatus* were collected on pieces of rock from Aberffraw, Anglesey; *Elminius modestus* on mussels attached to the piles of Bangor pier in the Menai Straits; *Balanus perforatus* on rock chippings from the coast of the Gower peninsula; and *B. amphitrite* on pieces of glass bottle from the warm docks at Swansea. All specimens were obtained during the winter.

Immediately after the sample had been collected, about 70 to 100 individuals of each species were examined for the presence of egg masses. Of the four species only *Elminius modestus* could not be obtained normally free of embryos in the cooler months of the year (Crisp & Davies, 1955). To obtain *E. modestus* without egg masses all the individuals settled on each *Mytilus* shell, except for one specimen of mature size, were removed. The isolated specimens so obtained were kept in separate dishes to prevent further fertilization and were fed for about a fortnight to encourage liberation (Crisp, 1956; Crisp & Spencer, 1958). Individuals which liberated nauplii during isolation were then certain to be empty, since self-fertilization does not occur in this species (Barnes & Crisp, 1956). They were then used to investigate the induction of further breeding. The other three species were found to be entirely free of egg masses at the season when the experiments were conducted.

About 20 to 30 individuals of each species were kept in 6 in. diameter glass crystallizing dishes and maintained at a series of different temperatures, each one varying by not more than ± 2° C. The temperatures were recorded each day throughout the experiments and a mean value calculated at the end.

Two identical groups of animals belonging to the same species were selected for each experiment at each temperature, except for *E. modestus* which had to be given a preliminary feeding as described above. One group was fed liberally on *Artemia* larvae and the other group was kept without food. The large quantities of *Artemia* larvae required were hatched from commercially available *Artemia* eggs in a warmed $3 \times 1\frac{1}{2}$ ft. glass tank containing sea water and continuously aerated to keep the eggs circulating throughout the tank. Hatched larvae were strained off, and transferred daily to the dishes containing barnacles, when fresh sea water, brought to the required temperature was added. Throughout the experiment the water surrounding the barnacles was freely aerated both to oxygenate it, and to keep the food moving over the barnacles, which then fed by simply extending the cirri (Southward & Crisp, 1959).

Cast skins, expelled egg masses and any liberations of nauplii were carefully noted, a separate record for each dish being kept. After an interval of 8–10 days at each temperature a few animals from each dish were examined to see whether any had become fertilized. If so, the stages of development of the fertilized egg masses were determined, using the categories given by Crisp

(1954). The condition of the ovary of all unfertilized specimens was visually determined, the stage of ovarian development being divided into five categories and points assigned as shown in Table 1. A mean ovary index was obtained for the samples taken from each dish.

TABLE 1. STAGES OF OVARIAN DEVELOPMENT

Condition of ovary	Ovary index score
Fertilized egg masses	4
Well-developed ovary filling mantle space	3
Moderately developed ovary	2
Slightly developed ovary with minute eggs	1
No ovarian development observed	0

The lengths and breadths of the fertilized eggs were measured in microns. Since the fertilized egg was approximately a prolate spheroid, the volume was calculated as $4/3\pi ab^2$, where $a = \frac{1}{2}$ length and $b = \frac{1}{2}$ breadth.

To study the influence of temperature on the size of released nauplii (stage I), normally fertilized *E. modestus* were collected from the field. Egg masses produced by each parent were divided into three batches, each of which was then incubated *in vitro* at different temperatures following the methods described by Patel & Crisp (1960). Immediately after being released stage I nauplii were preserved in 5% sea water formaldehyde and their dimensions measured.

These experiments were conducted during December 1957 to February 1958 and during December 1958 to February 1959, when the natural population of all the species was dormant and generally had poorly developed gonads. The results of both the years were identical and were therefore combined in the tabulated results.

EFFECT OF TEMPERATURE ON BREEDING

The results on the influence of temperature on the breeding activities of animals maintained at a series of different temperatures (as described above) are shown in Table 2. Breeding activity may be judged from the percentage of individuals fertilized at the end of the experiments at each temperature. It will be evident from Table 2 that the fed specimens of all the four species, though having scarcely any development of the gonads at the outset, developed gonads within a short time and soon reached breeding condition. In most cases they were able to breed after being kept for only 2–3 weeks at their breeding temperature. Both the percentage of the individuals carrying embryos and also, in general, the ovary index increased as the temperature was raised above the critical minimum value for breeding. This minimum varied with each species, thus *B. amphitrite* started breeding activity at 17–18° C, *B. perforatus* and *C. stellatus* at 15–16° C and *E. modestus* was found

TABLE 2. THE EFFECT OF TEMPERATURE AND FEEDING ON THE MEAN INDEX OF DEVELOPMENT OF THE OVARY, ON THE PERCENTAGE OF FERTILIZED INDIVIDUALS AND ON THE NUMBER OF BROODS IN BARNACLES

	Fed				Starved			
Mean temperature (°C)	No. of days animals were kept at stated temperature	% fertilized	Mean ovary index	No. of broods	No. of days animals kept at stated temperature	% fertilized	Mean ovary index	No. of broods
(a) *Chthamalus stellatus*								
32	15	10	2·1	1	25	0	1·0	0
30	15	36	2·7	1	—	—	—	—
28	15	30	3·1	1	25	0	1·2	0
25	25	20	3·6	1	35	0	1·0	0
20	25	60	3·4	1	35	0	1·0	0
15	25	12	2·7	1	35	0	1·0	0
9	35	0	1·6	0	—	—	—	—
6	40	0	1·2	0	40	0	0·5	0
(b) *Balanus perforatus*								
31·5	10	0	—	*	10	0	—	*
28·0	20	53	3·5	1	25	0	1·0	0
23·5	20	77	3·8	1	25	0	1·5	0
19·0	20	60	3·5	1	25	0	1·5	0
15·0	35	5	2·4	1	40	0	1·0	0
13·0	40	0	2·0	0	40	0	0·8	0
10·0	40	0	1·2	0	—	—	—	—
6·0	40	0	0·9	0	40	0	0·5	0
* Indicates specimens died within 8–10 days.								
(c) *Balanus amphitrite*								
31·5	40	100	4·0	2	45	0	0·5	0
27·5	40	100	4·0	2	45	0	0·5	0
24·5	40	100	4·0	2	—	—	—	—
22·5	40	100	4·0	2	45	0	0·7	0
19·5	20	73	3·6	1	—	—	—	—
17·5	20	34	3·0	1	45	0	1·0	0
14·5	45	0	2·0	0	45	0	0·8	0
11·5	35	0	2·0	0	—	—	—	—
7·5	35	0	1·0	0	—	—	—	—

(d) *Elminius modestus*

(All animals fed throughout experiment.)

Mean temperature (°C)	No. of days animals were kept at stated temperature	% fertilized	Mean ovary index	No. of broods
30	30	35	2·9	1
25	19	93	3·9	1
20	19	90	3·9	1
15	20	70	3·7	1
9	32	54	3·3	1

fertilized at 8°–9° C. Above the optimum temperature for breeding, the percentage of fertilized individuals and the mean ovary index fell. Thus *B. perforatus* bred at an optimum rate between 22° and 23° C, and continued to breed up to 27°–28° C. At even higher temperatures (30°–32° C) animals survived for only 7–10 days and did not breed. *C. stellatus* did not reach its optimum until 24°–25° C, and continued producing broods up to 30°–32° C, though a lower percentage of the population was found to be carrying eggs at this temperature. In *B. amphitrite* all the experimental individuals bred readily between 22° and 32° C, and on one occasion when the thermostat failed they withstood temperatures of the order 38°–40° C for over 24 h. Individuals of *E. modestus* reached their optimum rate at 22°–25° C, and both the percentage of fertilized individuals and the mean ovary index fell considerably at 30°–31° C.

EFFECT OF NUTRITION ON BREEDING

It can be seen from Table 2 that, within the characteristic temperature range of breeding for any given species, only those groups of individuals which were given food developed gonads rapidly and bred readily. When barnacles were fed on *Artemia* larvae the newly developed ovary assumed an abnormal pinkish tint instead of its usual yellow colour. Similar colour changes, but more pronounced, were observed in artificially fed *Lepas anatifera* (Patel, 1959). The operculate barnacles, unlike *Lepas* however, could live without food for long periods. These starved individuals failed to develop the gonads, as is evident from the continuing low mean ovary index. It should be borne in mind that these animals were collected at the season when the feeding activity and reserves were already at a minimum. Had they been collected just before the normal breeding season, when the gonads would have been more fully developed, a proportion at least of the observed specimens would doubtless have bred on raising the temperature. This was later found to be so with *C. stellatus* and *B. perforatus* during May and June, respectively.

To confirm that nutrition played a major role in allowing breeding to commence, some of the starved individuals of the species *B. amphitrite*, *B. perforatus* and *C. stellatus*, which had not fertilized even after having been kept for 30–40 days above the critical breeding temperatures, were fed liberally on *Artemia* larvae. Within 18–20 days these specimens entered the breeding condition and fertilized readily. The mean ovary index was also accordingly increased.

The temperature above which breeding begins in each species agrees well with the natural breeding season and the geographical distribution. *E. modestus* which breeds throughout the year in south-west England (Crisp & Davies, 1955) and whose distribution extends to the colder east coast of Britain, has the lowest critical breeding temperature of 8°–9° C. *C. stellatus*, which breeds only from May to September (Crisp, 1950) and whose distribution extends up the west and north coasts of Scotland but not to the east coast, has the next highest breeding temperature of 15°–16° C. *B. perforatus* has a breeding range whose lower limit is about equal to that of *C. stellatus*, but, since its habitat is lower on the shore, it does not benefit to the same degree as *C. stellatus* from the sun's heat and the increase in temperature that occurs in spring. This may explain its later onset of breeding (July) and its more restricted distribution, which extends only to St David's Head (Norris & Crisp, 1953). *B. amphitrite*, with a critical breeding point of 17°–18° C, is a more tropical form, found in Britain only in exceptionally warm areas, such as power station effluents, and does not occur on the open coast further north than the Charente area in the Bay of Biscay (Bishop, Crisp, Fischer-Piette & Prenant, 1957).

The upper temperature limits of breeding are not far removed from the upper limits of survival of each species. The most sensitive of the four was *B. perforatus* which could not survive temperatures in excess of 30° C for long, and ceased to breed in this range. *C. stellatus* survives at the level of high water springs where it may be exposed to temperatures of at least 38° C (Southward, 1955). This species continued to breed at 32° C but, as only 10% contained fertilized eggs at this temperature, it is unlikely that breeding would have continued at temperatures much in excess of this. *E. modestus*, which can survive at levels almost as high as those occupied by *C. stellatus*, was not tested above 30° C; the fall in the percentage fertilized at this temperature suggests, however, that its upper limit is close to that of *C. stellatus*. *B. amphitrite*, the species most tolerant of high water temperatures, showed no fall-off in breeding at 31·5° C, all individuals containing embryos.

INFLUENCE OF TEMPERATURE AND NUTRITION ON THE MOULTING RHYTHM

Crisp & Patel (1958, 1960) have reported that the frequency of moulting was dependent on the temperatures during and of nutrition prior to the experimental period. During the present series of experiments the frequency of moulting at different temperatures was measured for fed and starved individuals of all the four species. The results are illustrated in Fig. 1 in which the rate of moulting per barnacle per day is plotted against temperature, together with Southward's (1955, 1957) observations on their cirral activity.

The temperature optimum of moulting activity was generally slightly lower than that of cirral activity. The difference may well be explained by the difference in duration of the two types of experiments. Experiments on cirral beats could be completed in a much shorter time than those on moulting which required 10–15 days. At the upper limit of temperature tolerance, therefore, rates of cirral beat could be measured before the elevated temper-

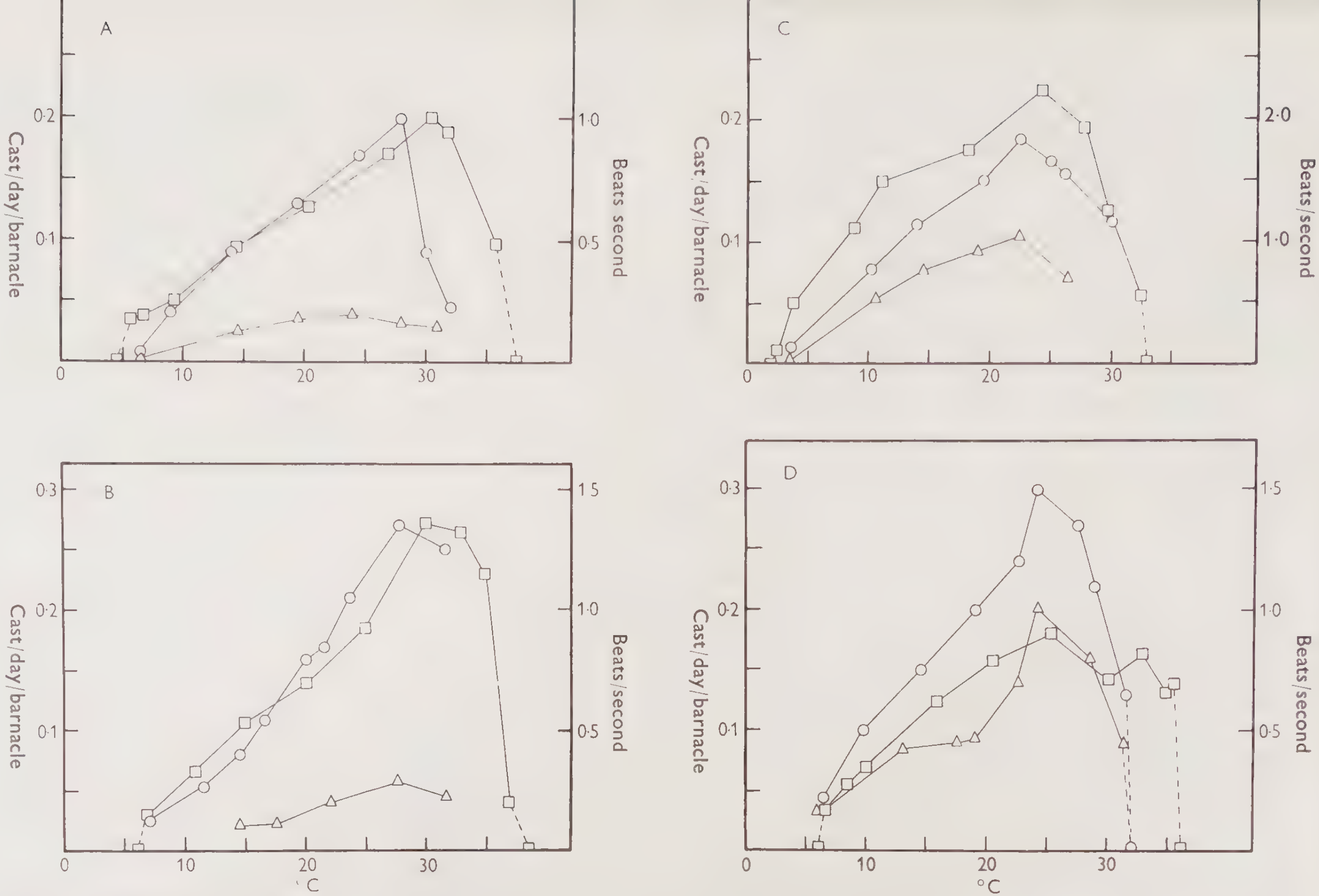

Fig. 1. Influence of temperature and nutrition on the moulting rhythm and the effect of temperature on the cirral activity (the latter is taken from Southward, 1955 and 1957) (*A*) *Chthamalus stellatus*, (*B*) *Balanus amphitrite* var. *denticulata*, (*C*) *Elminius modestus* and (*D*) *Balanus perforatus*. ○ Indicates moulting rate of fed specimens. △ Indicates moulting rate of starved specimens. □ Indicates the rate of cirral beating. (Note: In order to accommodate the high rate of beating in *Elminius modestus*, the scale on the ordinate of Fig. 1 *C* showing the rate of beat has been reduced in comparison with the scales in Fig. 1 *A*, *B* and *D*.)

ature had a harmful effect or had disturbed the animal's metabolism. On the other hand, by the end of a period of 2 weeks at high temperatures the animal may have consumed some of its food reserves and would then probably show a decline in its moulting rhythm (see Crisp & Patel, 1960).

It will be seen from Fig. 1 that the moulting rate of well-nourished individuals increased linearly with the temperature up to an optimum; above this optimum the moulting rate, like cirral activity, underwent a sharp drop. Thus in *C. stellatus* and *B. amphitrite* (Fig. 1 *A*, *B*) the moulting rate increased steadily from 7° to 28° C, in *B. perforatus* (Fig. 1 *D*) from 7° to 24° C, and in *E. modestus* the moulting rate increased linearly from 4° to 23° C (Fig. 1 *C*). The moulting rate of all the four species dropped markedly at yet higher temperatures of the order 29° to 31° C. Moreover, it will also be evident from the figure that the moulting rate of specimens kept without food was at all temperatures less than that of well-nourished individuals. Generally the effect of starvation on the moulting rhythm became more and more pronounced as the period of starvation was prolonged and the temperature increased, as was observed also in *Balanus balanoides* (L.) by Crisp & Patel (1960).

TABLE 3. TEMPERATURE OF THE SEA PRIOR TO COLLECTION, AND RATE OF CIRRAL BEATS

Species	Mean sea temperature over a period of 4 weeks before the specimens were collected (°C)	Rate of ciral beat prior to collection	Rate of cirral beat at maximum activity	Ratio of the activity prior to collection over the maximum activity
Elminius modestus	12	15·4	22·4	0·69
Balanus perforatus	12	5·0	9·0	0·55
Chthamalus stellatus	12	3·7	10·2	0·36
Balanus amphitrite	16	6·0	13·6	0·44

From Fig. 1 *C* and *D* it will also be seen that starved specimens of both *E. modestus* and *B. perforatus* showed a similar rise in moulting rate with temperature as was shown by liberally fed barnacles, but that this was not true of starved specimens of *C. stellatus* and *B. amphitrite*, which showed scarcely any significant rise in their moulting rate with the temperature (Fig. 1 *A*, *B*). In winter these two species were found to lack any sign of ovarian development, whereas *Elminius* continued to breed and *B. perforatus* generally had a rudimentary fatty ovary at the time of year that the experiments were carried out. Furthermore, the rate of cirral activity, compared with the maximum possible rate, would have been lower in *C. stellatus* and *B. amphitrite*. This is shown in Table 3, where the temperature in the natural habitat before collection and the rate of cirral beat (interpolated from Southward's results) is given. It seems likely therefore that, whereas *Elminius* *modestus* and *B. perforatus* may have been feeding at a sufficient rate to maintain their reserves in some degree, *C. stellatus* and *B. amphitrite* had been feeding more sluggishly in relation to their optimum, and were in a more starved condition. In consequence starved individuals of these two species were probably unable to maintain a moulting rate in step with the rise in temperature.

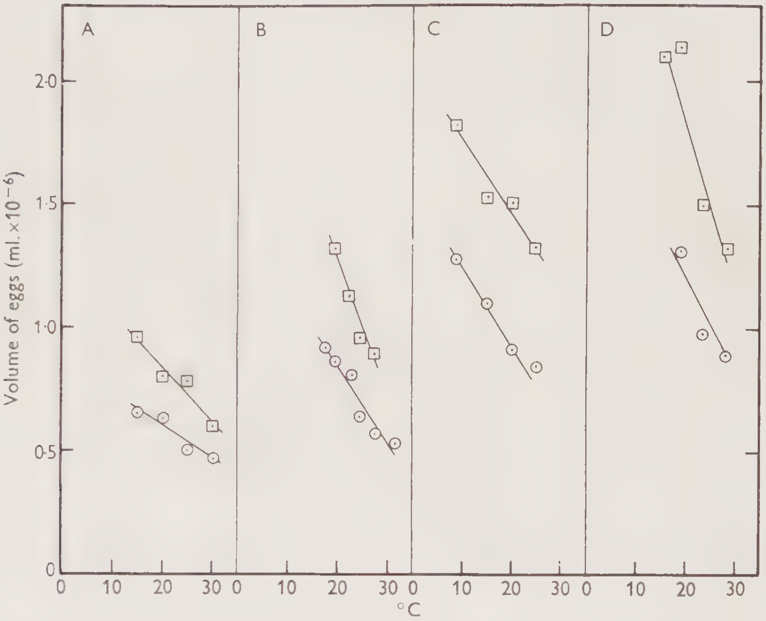

Fig. 2. Effect of temperature on the volume of eggs (*A*) *Chthamalus stellatus*, (*B*) *Balanus amphitrite* var. *denticulata*, (*C*) *Elminius modestus* and (*D*) *Balanus perforatus*. ⊙ indicates volumes of eggs containing early stage embryos. ⊡ Indicates volumes of eggs containing late stage embryos.

TEMPERATURE AND EGG SIZE

The dimensions of fertilized eggs from the adults kept and fed at a series of different temperatures during the period that the ovary and subsequent brood were developing, are given in Table 4. The mean lengths, breadths and deduced volumes are shown together with the corresponding standard errors. The egg volumes are plotted in Fig. 2, against the temperature of development. In all the four species at all temperatures the volume of the eggs increased as the embryos developed. Furthermore, the volumes of both early (stages 1 to 7) and late stages (stages 8 to 13) increased with the lowering of the temperature at which they had developed as ova. Generally, the breadth remained more or less constant but the length varied considerably. Identical results were reported by Patel (1959) in *Lepas anatifera*, and Crisp (1960) found a significant change in volume of the fertilized eggs of the boreo-arctic species *B. balanoides* collected from different latitudes. The size of the eggs decreased from north to south, i.e. from colder to warmer water. Earlier Crisp (1954) had shown that the dimensions of fertilized eggs in boreo-arctic species of operculate cirripedes were in general larger than those of their relatives from the lower latitudes. The measurements given in Table 4 are approximately of the same value as given by Crisp (1954) at the nearest comparable temperature.

TABLE 4. INFLUENCE OF TEMPERATURE ON SIZE AND THE VOLUME OF EGGS CONTAINING EMBRYOS OF BARNACLES

	Stages 1–7			Stages 8–13		
Mean temperature (°C)	Length (μ)	Breadth (μ)	Volume (ml. × 10^{-6})	Length (μ)	Breadth (μ)	Volume (ml. × 10^{-6})
			(*a*) *Chthamalus stellatus*			
30	132 ± 5·4	83 ± 0·8	0·47	154 ± 2·4	87 ± 1·3	0·60
25	144 ± 1·7	82 ± 0·2	0·50	168 ± 0·3	94 ± 0·2	0·78
20	163 ± 1·8	86 ± 0·2	0·63	173 ± 1·2	94 ± 0·2	0·80
15	165 ± 1·6	87 ± 0·25	0·65	184 ± 4·3	99 ± 2·2	0·95
			(*b*) *Balanus perforatus*			
28·0	161 ± 4·2	103 ± 1·8	0·91	193 ± 5·0	115 ± 2·2	1·33
23·5	170 ± 1·8	105 ± 0·24	0·98	211 ± 3·2	117 ± 1·2	1·50
19·0	194 ± 1·8	114 ± 0·2	1·32	238 ± 3·7	131 ± 1·6	2·14
15·0	—	—	—	245 ± 8·5	127 ± 3·6	2·10
			(*c*) *Elminius modestus*			
25	184 ± 1·4	94 ± 0·5	0·85	214 ± 1·25	109 ± 0·8	1·33
20	189 ± 5·8	97 ± 0·5	0·93	226 ± 1·25	113 ± 0·78	1·51
15	202 ± 1·7	102 ± 0·65	1·10	232 ± 1·80	112 ± 0·86	1·53
9	214 ± 2·6	107 ± 0·84	1·28	241 ± 4·0	120 ± 2·60	1·82
			(*d*) *Balanus amphitrite*			
31·5	127 ± 6·0	88 ± 2·0	0·53	—	—	—
27·5	136 ± 3·7	89 ± 0·3	0·57	162 ± 5·0	103 ± 3·0	0·90
24·5	145 ± 3·5	92 ± 0·4	0·64	173 ± 2·0	103 ± 1·4	0·96
22·5	159 ± 2·8	99 ± 0·2	0·81	178 ± 2·8	110 ± 1·2	1·13
19·5	165 ± 1·5	100 ± 1·2	0·86	184 ± 3·0	117 ± 1·4	1·32
17·5	167 ± 2·4	102 ± 0·8	0·92	—	—	—

It will be seen that in three of the four species the influence of temperature on egg size is accentuated in the later embryonic stages, though the curve for *E. modestus* (Fig. 2*C*) has a similar slope for both early and late stages. If egg size was related to the size of the developing embryo these changes in slope suggest that temperature influences not only the initial size of the ova but also the amount of embryonic growth, both effects determining the ultimate size which the developing embryo can attain. In order to test the influence of temperature during development on the ultimate size of the embryo, fertilized eggs of *E. modestus*, which had been oviposited by the same parent in July at the prevailing sea temperature, were incubated *in vitro* at a series of different temperatures. The first stage nauplii formed showed a variation in size (Table 5). That those which developed at the highest temperature were the smallest in size confirms that in barnacles the embryos are reduced in size if they undergo embryonic development at a higher temperature.

Our results agree with those obtained by Gray (1928*a*, *b*) who, in an essentially similar experiment reported that the eggs of *Salmo fario* from the same female, when incubated at a series of different temperatures hatched into fry of different size. Those reared at a higher temperature were smaller than those incubated towards the lower limit of normal development. However, both our findings and Gray's differ from those of Loosanoff (1959) who used eggs of *Venus* (*Mercenaria*) *mercenaria* which had been artificially induced to spawn during winter. The spawn was maintained at a series of different temperatures. Loosanoff found no significant difference in the final size of the larvae at the time of settlement. However, the results in Fig. 2 of his paper show a drop in size as the temperature was raised above 20° C and the failure to observe any size difference may have been due to the great variation in the larval size at each temperature.

TABLE 5. INFLUENCE OF TEMPERATURE ON LENGTHS AND BREADTHS OF STAGE I NAUPLII OF *ELMINIUS MODESTUS*. EGG MASSES REMOVED FROM ONE PARENT WERE INCUBATED *IN VITRO* AT THE FOLLOWING DIFFERENT TEMPERATURES

Parent no.	Stage of development of embryos at beginning of experiment	11° C		16° C		23° C	
		Length (μ)	Breadth (μ)	Length (μ)	Breadth (μ)	Length (μ)	Breadth (μ)
1	3–4	268 ± 1·5	116 ± 0·5	252 ± 2·5	115 ± 0·6	229 ± 3·9	108 ± 1·3
2	6–7	259 ± 1·1	118 ± 0·9	247 ± 2·6	114 ± 0·8	232 ± 5·6	112 ± 1·4
3	8–9	260 ± 1·1	118 ± 1·2	252 ± 2·0	119 ± 2·4	246 ± 0·5	114 ± 0·7

The effect of temperature on egg size is common to many other groups of animals. Moore (1942) found eggs of graded diameter in different species of frogs belonging to the genus *Rana*, the northern forms laying larger eggs than the southern forms. Later the same author reported similar differences in the diameter of fertilized eggs of *Rana pipiens* inhabiting different latitudes (Moore, 1949). Colder conditions not only increase the size attained by the embryos but in many animals lead also to a larger size in the adults. Many observers have noticed that marine organisms belonging to the same species but inhabiting different latitudes grow more slowly but attain a significantly larger size in higher latitudes (for literature see Gunter, 1950, 1957).

Although the amount of growth is less at higher temperatures, the rate at which the final condition of maturity is reached is greater, whether the system be a developing oocyte, an embryo, or an adult poikilotherm. Gray's simple and direct explanation for embryos was based on the fact that in this system only a limited amount of nutrient was available as yolk. If the growing tissue requires proportionately more energy for maintenance at a higher temperature, less material would inevitably be left over for growth. An exactly analogous explanation for developing oocytes or for adult animals cannot be sustained because in these systems the amount of living matter could, if necessary, be augmented during development to allow for increased metabolic activity. Moreover, even in embryos, there is no obvious reason why rapid development over a shorter time interval should be less efficient and so use more reserve food than slow development over a longer time. In barnacles the size of developing ova does not appear to depend to any significant extent on the nutrition of the parent, for animals which are poorly fed produce fewer, but not necessarily smaller, eggs.

It seems possible that in all three systems development may be controlled by similar basic processes in which the temperature coefficient of differentiation, leading to maturity, is greater than the temperature coefficient of tissue multiplication or growth. These two processes, differentiation and growth, do not therefore keep exactly in step at all temperatures; at low temperatures differentiation is relatively slower leading to a larger mature size, while at high temperatures growth is rapid leading to a smaller size at maturity.

We are grateful to Prof. E. W. Knight-Jones of the Department of Zoology, Swansea, for obtaining for us specimens of *B. perforatus* and *B. amphitrite*, and to Dr E. Naylor for supplying us with temperature records of Queen's Dock and other places around the Gower peninsula.

SUMMARY

Tropical species of operculate cirripedes, including *Elminius modestus* Darwin, *Chthamalus stellatus* (Poli), *Balanus perforatus* Bruguière and *B. amphitrite* var. *denticulata* (Broch), collected during the winters of 1957 to 1959, were induced to breed by raising the temperature and feeding liberally on *Artemia* larvae. Well-nourished specimens of *B. perforatus* and *C. stellatus* commenced to breed after being kept for 2–3 weeks at 15°–16° C; *B. amphitrite* required a temperature of 17°–18° C, whereas *E. modestus* bred at 8°–9° C. The percentage of the specimens bearing embryos increased with the temperature and reached optima lying in all four species between 22° and 25° C. The animals continued to breed, though less efficiently, up to temperatures of the order 28°–30° C, the limits varying a little for each species. Only fed individuals produced gonads and broods; those kept without food showed no breeding activity at any temperature even after 4–5 weeks, but after being fed for 2–3 weeks bred readily. The moulting rate of all four species was dependent both on temperature and on their prior nutrition. The moulting rate of well-fed specimens increased linearly to an optimum and subsequently dropped sharply. The moulting rhythm followed a pattern in relation to temperature

like that of cirral activity, but generally with a lower optimum temperature. The volume of the fertilized eggs increased during development and was greater the lower the breeding temperature.

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RED BLOOD VALUES IN THE PLAICE (*PLEURONECTES PLATESSA* L.)

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(Text-fig. 1)

The work reported in this paper forms part of a programme of investigation into the normal parameters of radiosensitive tissues in the plaice. The work was conducted prior to investigations into the effects of ionizing radiations on these tissues, in order to form a background to examinations of fish from areas of radioactive pollution resulting from the controlled disposal of radioactive effluent. Tissues were selected on the basis of known radiosensitive tissues in mammals and the work on red blood values reported here arose from these preliminary investigations.

In the first instance it was realized from the work of Schaefer (1925), Kawamoto (1929), Yokoyama*, Dombrowski (1953), Antipova (1954) and Kaplan & Crouse (1956), that the value of such indices of the red blood picture as packed cell volume (PCV), red cell count (RBC) and haemoglobin (Hb) might vary both with the size of the animal and with season. A preliminary investigation was therefore carried out in April 1956, using PCV as the index, to determine at what size asymptotic values for red blood were reached. This was followed in 1957 by measurement throughout the year of PCV, RBC, Hb and sedimentation rate (SR) in order to determine the existence and extent of seasonal variation, among fish that were large enough to have reached asymptotic values for red blood.

MATERIALS AND METHODS

The relationship between PCV and size was determined in April 1956 from a sample of 108 freshly caught live plaice. Seasonal variation was determined from samples of twenty to thirty freshly caught live plaice, obtained off Lowestoft at approximately 2-month intervals from the end of February to the beginning of September, together with a final sample examined at the beginning of December. A sample of 0·5 ml. of blood was removed from each fish, by cardiac puncture (Yoffey 1929), using a heparinized 1 c.c. glass syringe with No. 19 needle, and sufficient quantities of blood were transferred to a clean paraffin waxed watch glass for each measurement. Using standard techniques (Kolmer, Spaulding & Robinson, 1938), packed cell volumes were measured with Wintrobe microhaematocrit tubes. Red-cell counts were carried out using standard red-cell pipettes and a Hawksley improved Neubauer crystallite counting chamber. Fifty per cent filtered sea water is isotonic with plaice erythrocytes and was used as diluting fluid. It was just coloured with gentian violet to provide sufficient coloration of the cells to facilitate counting. The fluid was freshly filtered prior to each dilution, to remove precipitated stain.

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* Yokoyama, H. O. Studies on the origin, development and seasonal variation in the blood cells of the perch (*Perca flavescens*). Ph.D. Thesis, Univ. Wisconsin, 150 pp., 1947.

Haemoglobin estimations were made by the alkaline haematin method (Gibson & Harrison, 1945), using the B.D.H. artificial standard and a photoelectric absorptiometer. Sedimentation rates were measured by standard techniques, using microsedimentation tubes. During the early determinations of sedimentation rate measurements were made every fifteen minutes for 1 h, but in later determinations only the hourly rate was recorded.

PACKED CELL VOLUME AND WEIGHT

The data obtained on the relationship between PCV and weight are set out in Table 1. There is an increase in mean PCV with increase in weight of the fish up to a weight of approximately 120 g, when the PCV value stabilizes.

TABLE 1. RELATION BETWEEN PACKED CELL VOLUME AND WEIGHT. DATA FROM A SAMPLE OF FRESHLY CAUGHT LIVE PLAICE, APRIL 1956

No. of fish in sample	Weight range (g)	Mean weight of sample (g)	Mean PCV (%)	Range PCV % in sample	Standard deviation PCV
11	1– 20	14·1	17·2	14·1–20·6	2·2
16	21– 40	32·9	19·5	15·3–23·8	2·8
15	41– 60	52·0	21·9	19·2–24·6	1·7
12	61– 80	72·3	22·9	19·2–26·7	2·4
14	81–120	97·5	25·8	20·1–30·2	3·0
9	121–150	136·0	25·7	15·3–31·5	6·0
8	151–200	174·6	25·0	20·5–32·2	4·3
13	201–300	247·9	25·6	18·0–32·1	4·5
10	301–500	374·2	24·7	20·4–27·7	2·4

Inspection of the data in Table 1 shows that there is a considerable variation about the mean value for PCV, percentage variation ranging from 24 to 62%, which is not uncommon in the determination of PCV in fish blood. Field, Elvehjem & Juday (1943) give percentage variations of 61% for carp blood and 50% for trout blood, and Young (1949), measuring the PCV of individual fish at time intervals of from 10 to 14 days, remarks that the variation in PCV of individual fish at different times is comparable to that between different fishes of the same species at the same time. He gives percentage variation figures of from 15 to 67% of the mean PCV.

The increase of RBC values with increase in size of the fish has been noted before by Dombrowski during a study of the blood of the carp. He found that the erythrocyte counts increased from 1·1 × 10^6 per mm^3 at hatching to 1·5–1·8 × 10^6 per mm^3 at the end of the fourth season, a mean increase of 50%, and that this was accompanied by an increase in haemoglobin from values of 7·3 g 100 ml. to 10·8 g 100 ml. over the same period, an increase of 48%. The increase in mean PCV in the plaice over the weight range 14–120 g (a 3–4 year period) is comparable, i.e. 17·2–25·6, an increase of 49%.

From the preceding plaice data it was decided to confine the study on seasonal variation to fish of not less than 140 g, so as to obviate the fluctuations due to differences in size of the fish. The data that follow are accordingly only applicable to plaice of weights in excess of 140 g.

SEASONAL VARIATION IN RED BLOOD VALUES

The data on seasonal variation of PCV, RBC, Hb and SR given in Table 2 and Fig. 1 show clearly that a process of haemoconcentration occurs throughout the late spring and summer, and that this is followed in the late summer and autumn by haemodilution.

TABLE 2. SEASONAL VARIATION IN RED BLOOD VALUES: PACKED CELL VOLUME (PCV), RED BLOOD CELL COUNT (RBC), HAEMOGLOBIN (Hb) AND SEDIMENTATION RATE (SR), DURING 1957

	Date of sample				
Parameter	28 February	23 April	21 June	29 August	1 December
No. observations	28	26	22	26	24
PCV Range (%)	16·7–27·5	16·2–27·2	22·2–32·2	20·6–32·4	17·4–27·0
Mean (%)	21·4	21·8	27·0	25·6	21·3
Standard deviation	2·9	3·0	3·1	3·3	2·7
No. observations	29	25	22	26	20
RBC Range (10^6/mm^3)	1·52–2·81	1·53–2·54	1·86–2·62	1·79–3·01	1·72–2·42
Mean (10^6/mm^3)	2·05	2·02	2·28	2·38	2·03
Standard deviation	0·35	0·28	0·22	0·29	0·20
No. observations	29	26	22	26	21
Hb Range (g/100 ml.)	5·52–11·06	4·55–7·87	6·70–10·42	4·38–8·51	4·22–6·85
Mean (g/100 ml.)	8·12	5·66	8·75	6·37	5·93
Standard deviation	1·38	0·88	1·03	1·03	0·66
No. observations	26	25	20	20	20
SR Range (mm/hr)	1·0–2·75	0·7–2·05	0·5–1·8	0·3–1·65	0·7–1·75
Mean (mm/hr)	1·65	1·37	1·01	0·96	1·14
Standard deviation	0·49	0·35	0·37	0·34	0·28

The values for PCV and RBC reach their lowest points, in the period examined, at the end of the winter and then increase fairly rapidly during the early summer. The increase in PCV from April to June is rather more rapid than the increase in RBC, and the plasma volume is thus decreasing slightly over the period, i.e. the blood is becoming more concentrated. SR—which is some measure of the concentration of the blood, the rate slowing as the

RBC increases—is consistent with these changes by its significant decline over the same period. It can be calculated from Table 2 that there is no significant difference between PCV values in June and August, nor in RBC over the same period. These values are therefore probably steady during the

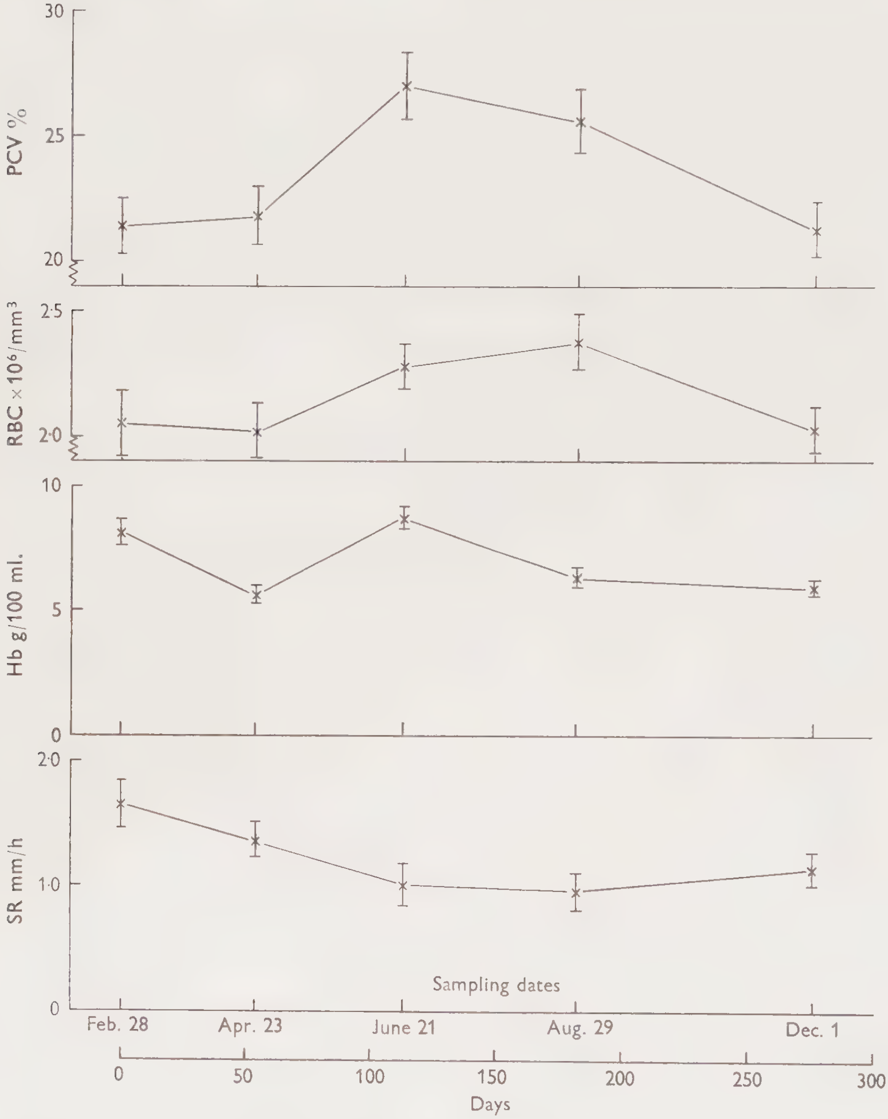

Fig. 1. Variation of plaice red blood values with season; packed cell volume (PCV), red blood cell count (RBC), haemoglobin (Hb), and sedimentation rate (SR), during 1957. The vertical lines show ± twice the standard error of the mean.

summer months, as is the SR, which halts its rapid fall and levels out over this period. From August to December both PCV and RBC fall steadily and the SR increases as the blood becomes more dilute.

It is interesting to note that the concentration of the blood revealed by the relative changes in PCV and RBC from April to June, is foreshadowed by a significant decrease in mean SR over the period February to April.

The values for Hb afford a less clear picture of events, in that they are already high at the end of the winter, falling to their lowest value of the whole period during the early spring. From then on they follow the same general trend as PCV and RBC, though their decline, which commences in June, is somewhat earlier than the decline in RBC.

A similar picture of haemoconcentration is described for another poikilotherm, the frog, by Kaplan & Crouse, though the time and magnitude of events are somewhat different, and the spring spawning obviously interrupts the rhythm.

It seems unlikely that the haemodilution which occurs in the plaice throughout the autumn and winter is a direct result of the decreased food intake occurring at this time. Schaefer, using pumpkin seed fish (*Eupomotis gibbosus* L. Cuvier and Valenciennes), found that these fish exhibited haemodilution during the late autumn and winter, but that the blood was able to concentrate again during the spring in spite of starvation throughout the whole period under investigation.

From the work of Musacchia & Sievers (1956), on cold torpor in the turtle (*Chrysemys picta*), it seems that the mechanism behind these changes is basically one of temperature. They found that turtles subjected to a low environmental temperature, 2 ± 4° C, exhibited haemodilution and that this was particularly well shown by the rapid fall in PCV and whole blood specific gravity. Thus the concentration of the blood of the plaice in late spring and summer may be a response to an increase in water temperature, and the subsequent haemodilution later in the year, the result of a falling water temperature.

ABNORMAL SEDIMENTATION RATES

It is well known that in mammals some disease conditions are accompanied by an accelerated SR; this has also been reported by Schumacher, Hamilton & Longtin (1956) for brook trout with furunculosis. These authors commented on the future of the method as a diagnostic tool in fish hatcheries and stressed the necessity for further information with respect to additional species and disease conditions.

During the early months, February and April, of the 1957 sampling programme some plaice were obtained exhibiting necrosis of the caudal fins and the posterior margins of the dorsal and ventral fins. When sedimentation rates were determined for these fish they proved to be abnormally fast (see Table 3).

TABLE 3. ABNORMAL SEDIMENTATION RATES, OF FISH WITH FIN NECROSIS, COMPARED WITH NORMAL FISH, FROM FEBRUARY AND APRIL 1957 SAMPLES

	Sedimentation rate			
	Healthy fish		Fish with fin necrosis	
Time of observations (min)	Range (mm)	Average (mm)	Range (mm)	Average (mm)
15	0·1–0·8	0·3	1·0–1·2	1·1
30	0·4–1·6	0·8	2·0–2·9	2·5
45	0·8–2·5	1·4	2·9–5·8	4·6
60	0·8–3·5	1·7	4·0–7·8	6·2

It is a pleasure to record my thanks to Mr F. Morgan who initiated and guided this work and to Mr C. Barker for his help throughout.

SUMMARY

The present study was undertaken as part of a programme designed to measure various parameters of normal fish tissues, prior to an investigation into the effects of ionizing radiation upon these tissues. The tissues were selected on the basis of known radiosensitive tissues in mammals. It was found that red blood values for the plaice, as indicated by packed cell volume, increased with the weight of the fish, up to a weight of approximately 120 g. Seasonal variations in packed cell volume, red blood cell count, haemoglobin and sedimentation rate among fish of not less than 140 g in weight were examined. A process of haemoconcentration during the spring and summer and one of haemodilution during the autumn and winter occurred. Data on accelerated sedimentation rates among diseased plaice are recorded.

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ON THE TOLERATION OF ANAEROBIC CONDITIONS BY *CALIGUS DIAPHANUS* NORDMANN

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Many free-living and parasitic invertebrates have been known to tolerate low oxygen tensions and anaerobic conditions. Von Brand (1946) who reviewed the extensive literature on anaerobiosis in invertebrates listed species of *Cyclops* which under experimental conditions could tolerate 2–18 h of anaerobiosis. Apart from this, few experimental studies have been made on anaerobiosis in copepods, especially the parasitic species. Availability of a number of live *Caligus diaphanus* at Plymouth made it possible to make a few preliminary observations on the behaviour of this copepod parasite under anaerobic conditions.

MATERIAL AND METHODS

Gurnards (*Trigla* sp.) examined at Plymouth, were found to be infected by *Caligus diaphanus* Nordmann, the parasite being usually found on the inner side of the operculum. Although over a hundred gurnards were examined it was possible to obtain only ten parasites.

Experimental anaerobic conditions were produced by bubbling oxygen-free nitrogen from a cylinder into sea water. The nitrogen was first passed through a wash-bottle containing alkaline-pyrogallol to remove any traces of oxygen. Estimations of dissolved oxygen using Winkler's method usually gave a value which was equivalent only to that found dissolved in the reagents. Bubbling nitrogen for 40 min usually produced very low oxygen tensions. Four parasites were transferred to a small glass-stoppered bottle (30 ml. capacity) and flushed with oxygen-free sea water under liquid paraffin. The glass stopper was inserted and smeared with stop-cock grease to prevent air leaking into the bottle. The bottles were immersed in a trough of water kept at room temperature (18° C). A similar number of animals in identical bottles with fresh sea water served as control.

C. diaphanus when left in fresh sea water usually attaches itself to the sides or to the bottom of the container. The urosome of the animal is usually slightly tilted at an angle and shows periodic movement. The thigmotactic behaviour of the parasite in remaining attached to the surface of the container was used as a measure of behaviour under low oxygen tensions. *Caligus* is

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also slightly transparent and the anal peristalsis could be easily observed in live animals. This was used as an indication of the recovery of these animals after transferring to fresh sea water from anaerobic conditions.

When exposed to anaerobic conditions, the animals usually become detached and lie inactive at the bottom of the container although anal peristalsis continues. Under anaerobic conditions the time taken by the animal to become detached varied from 10 min to 4 h. The results are tabulated in Table 1.

TABLE 1. TOLERATION OF ANAEROBIC CONDITIONS BY *CALIGUS DIAPHANUS*

Time of exposure of anaerobiosis	No. of animals		
	Active and attached	Moribund	Dead
10 min	4	—	—
10 min	4	—	—
20 min	4	—	—
30 min	2	—	—
30 min	4	—	—
45 min	—	4	—
1 h	—	2	2
1 h	4	—	—
1½ h	4	—	—
2 h	4	—	—
2 h	2	—	2
3 h	2	—	1
3 h	—	2	2
4 h	1	3	—
4 h	1	3	—
8 h	—	—	4
9 h	—	—	4

Note: Three types of reaction were used as arbitrary criteria in these experiments. (1) active and attached; (2) moribund, i.e. lying inert on the bottom but showing anal peristalsis. (3) dead, i.e. not reacting to mechanical stimuli. Four animals were used in each experiment; four animals in fresh sea water served as control.

TABLE 2. THE TIME TAKEN FOR RECOVERY OF *CALIGUS DIAPHANUS* AFTER A PERIOD OF ANAEROBIOSIS

No. of animals	Duration of anaerobiosis (h)	Time taken for complete recovery (min)
2*	3	2
1	3	4
1	3	2
2*	3	2
2	3	3
2	4	No recovery
1	4	15
2	4	15
2	4	10
2	8	20
1	9	30

Note. In a few instances owing to shortage of material, the same animals had to be used in more than one experiment. (These experiments are shown with an asterisk.) The use of the same animals did not cause any variation.

On transferring to fresh sea water over 60% of the parasites recovered. The time taken for complete recovery, i.e. for the animal which lies moribund to be attached again varied from 2 to 30 min, depending on the time of exposure to anaerobic conditions (Table 2). The animals under anaerobic conditions for 3 h recovered in 2–3 min, while animals exposed to similar conditions for 4 h recovered in 4–15 min. Prolonged exposure of 8 and 9 h duration (in two experiments) resulted in the animal recovering after a period of 20–30 min.

The results would tend to show that *C. diaphanus* is capable of enduring anaerobic conditions without apparent ill effects.

I wish to thank Prof. J. E. G. Raymont, Professor of Zoology, University of Southampton, for several valuable suggestions and the Director and Staff of the Marine Biological Laboratory, Plymouth, for all the facilities given while working there.

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ON THE PIGMENTS OF THE CHRYSOPHYCEAE

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(Text-figs. 1–3)

The colour of the chromoplasts in the Chrysophyceae varies from a greenish yellow to a golden brown. Klebs (1892) described this colour as being due to a special pigment which he called 'chrysochrom'. Gaidukov (1900) made an acetone extract of a dense bloom of *Chromulina rosanoffii* (Woronin, 1880) Bütschli, filtered from the tanks in the cold glasshouses of the Botanic Gardens in St Petersburg. He found a water soluble pigment which he called 'phycochrysin' together with 'chrysochlorophyll' and 'chrysoxanthophyll'. Most authors have since questioned the existence of special pigments in the Chrysophyceae (Fritsch, 1937; Smith, 1938). Carter, Heilbron & Lythgoe (1939) analysed extracts of an incrustation of *Apistonema carteri*, *Thallochrysis litoralis* and *Gleochrysis maritima* (identified by F. E. Fritsch) found on the chalk cliffs at Folkestone, and identified β-carotene, fucoxanthin and lutein, using calcium carbonate as adsorbent in their analysis. Heilbron (1942) later drew attention to the fact that these pigments are present in the Bacillariophyceae but not in the Xanthophyceae, throwing doubt on Pascher's view of the close relationship of all three groups. We now know that it is not lutein but diadinoxanthin that is present in the Bacillariophyceae (Strain, Manning & Hardin, 1944). Seybold, Egle & Hülsbruch (1941) then showed that the chlorophyll present in *Hydrurus foetidus* and *Chromulina rosanoffii* was chlorophyll *a*, apparently without other chlorophylls. Seybold (1941) has commented further on the singular occurrence and implications of chlorophyll *a* alone, and this has been recently discussed by Allen (1958). In recent years our knowledge of the pigments of the algae has been greatly advanced by Strain and his colleagues (Strain, 1958) but, while the pigments of the Xanthophyceae and Bacillariophyceae have been examined with the improved techniques now available (Pace, 1941; Strain, Manning & Hardin, 1943, 1944; Strain, 1958), those of the Chrysophyceae have not.

This paper does not represent a complete account of the pigments occurring in these organisms, but results presented here are of interest in view of the relationship of the Chrysophyceae with other algae.

METHOD AND MATERIAL

The pigments of eight species have been analysed. Unialgal cultures were grown for some weeks until a density sufficient to give good extracts was obtained. In most instances about 4–6 l. of culture after 6 weeks of (winter) growth was adequate. The organisms were centrifuged, treated with distilled water to extract any water-soluble pigments, recentrifuged and then extracted with acetone. The acetone extract was taken into light petroleum (B.P. 40–60°) and separated into epiphasic and hypophasic fractions with 90% methanol, the methanolic layer being twice extracted with light petroleum, and the petrol layer similarly extracted with 90% methanol. The hypophasic pigments were driven into diethyl ether by addition of water. Both phases were evaporated to dryness and redissolved in light petroleum. The epiphase was chromatographed on activated alumina or magnesium oxide, the column being developed by addition of acetone to the light petroleum. The hypophase was chromatographed on sugar (Tate and Lyle icing sugar containing $1\frac{1}{2}$% calcium phosphate) and the column developed by dropwise addition of *n*-propanol to the light petroleum. The bands in each case were eluted and portions evaporated and redissolved in hexane and carbon disulphide (epiphasic) or ethanol and carbon disulphide (hypophasic) for examination in a Unicam S.P. 500 spectrophotometer. The chlorophylls were examined in light petroleum.

The following species from the Plymouth cultures have been examined:

	Plymouth no.
Pseudopedinella sp.	167
Phaeaster-type with haptonema	168
Pavlova gyrans Butcher	93
Isochrysis galbana Parke	I
Phaeocystis pouchetii-motile *Prymnesium* stage	147
Chrysochromulina ericina P. & M.	25
Dicrateria inornata Parke	B
Hymenomonas sp.	156

In addition, extracts of the diatom *Phaeodactylum tricornutum* Bohlin and of *Dunaliella tertiolecta* Butcher, a chlorophycean, were also analysed in the same manner to provide specimens of other xanthophylls for running mixed chromatograms with those of the Chrysophyceae.

RESULTS

Cultures of *Isochrysis galbana* were analysed on five or six different occasions and this species has been studied in more detail than the others.

In every species all the pigment was extractable by acetone and was soluble in light petroleum; no water-soluble pigments were found either on the preliminary treatment with distilled water, or when the hypophase was re-extracted with diethyl ether.

ISOCHRYSIS GALBANA

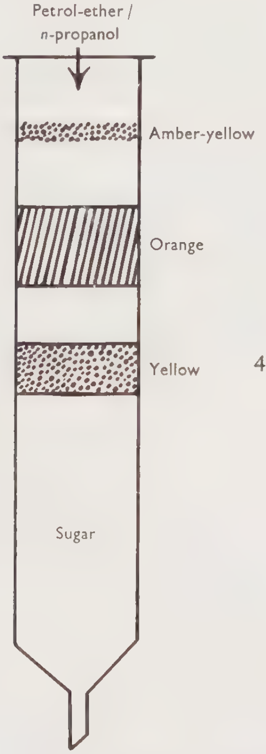
Epiphase

Careful development and slow elution of the bands formed on alumina or magnesium oxide showed that α-, β- and γ-carotenes were present. All the chlorophyll appeared to be chlorophyll *a*, strongly adsorbed above the carotenes and showing maxima at 430, 612 and 660 mμ in light petroleum. The addition of a trace of acetone to the developer caused a light yellow band to separate and move rapidly down the column. This band showed peaks at 445 and 474 mμ in hexane and 477 and 504 mμ in carbon disulphide, characteristic of α-carotene. Further addition of acetone separated the remaining carotene into a main orange band slowly passing down the column, and showing peaks at 451 and 478 mμ in hexane, 485 mμ in carbon disulphide (β-carotene), and a narrower red band above with the main peaks at 461 mμ in hexane and 496 mμ in carbon disluphide, resembling γ-carotene. Chromatography using magnesium oxide effected a better separation than on alumina, when both β-carotene and γ-carotene exhibited the upper maxima characteristic of these compounds.

Hypophase

If extraction and chromatographic analysis were performed rapidly, three yellow or orange bands were obtained on the sugar column on development with *n*-propanol: light petroleum mixtures (Fig. 1). Any chlorophyll washed through first; it always showed the spectrum of chlorophyll *a*. The main orange band resembled fucoxanthin in colour and position on the column, and in having a single absorption maximum (446 mμ) in ethanol with only a slight inflexion near 470 mμ. The suspected fucoxanthin exactly resembled that of *Phaeodactylum*, and a mixed chromatogram of the suspected fucoxanthin from *Isochrysis* and a specimen prepared by a similar separation on icing sugar of the xanthophylls of *Phaeodactylum* did not separate. The spectrum of each was similar (Fig. 2). The lower, yellow band could, from its spectrum, be either lutein or diadinoxanthin. A mixed chromatogram was run with a specimen of lutein prepared from *Dunaliella*, when the two pigments separated again on the column, indicating that the pigment was not lutein. When mixed with diadinoxanthin prepared from *Phaeodactylum*, however, no separation occurred when washed down a sugar column with the appropriate *n*-propanol: light petroleum mixture. The *Isochrysis* pigment also separated when run against violaxanthin from *Dunaliella*.

The two main xanthophylls of *Isochrysis* are, therefore, fucoxanthin (the main pigment) and diadinoxanthin (Fig. 3). The amber band above the fucoxanthin also exhibited a single broad peak in ethanol and was presumably an isomer (neofucoxanthin). If extraction and analysis extended over a long period, an additional yellow band was sometimes obtained below the diadinoxanthin. This could, from its position on the column, be diatoxanthin, but its absorption spectrum and colour resembled diadinoxanthin and it probably represented an artifact.



	Absorption maxima (mμ)		Pigment
	In ethanol	In carbon disulphide	
Amber-yellow	445	475 504	neofucoxanthin
Orange	446	475 506	fucoxanthin
Yellow	425 445 476	442 474 506	diadinoxanthin

Fig. 1. Chromatographic separation of the hypophasic pigments of *Isochrysis*.

OTHER SPECIES

A similar analysis of the other species produced substantially the same chromatographic picture, though mixed chromatograms have not been run in every case. Chlorophyll *c* was not detected and chlorophyll *a* appeared to be the only chlorophyll present. In the hypophasic fraction of each the two main pigments were fucoxanthin and diadinoxanthin, the fucoxanthin showing maxima in ethanol:

448 mμ from culture no.	167, 168
447 mμ	25, B
449 mμ	156

These maxima are lower than that found by Strain *et al.* (1944)—453 mμ—but the mixed chromatograms with *Phaeodactylum* fucoxanthin (447 mμ) suggest

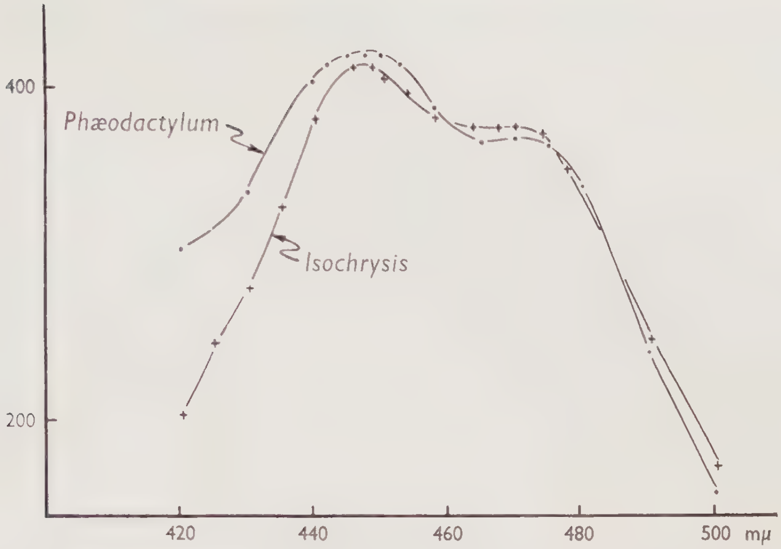


Fig. 2. Absorption spectra of fucoxanthin from *Phaeodactylum* and *Isochrysis* in ethanol.

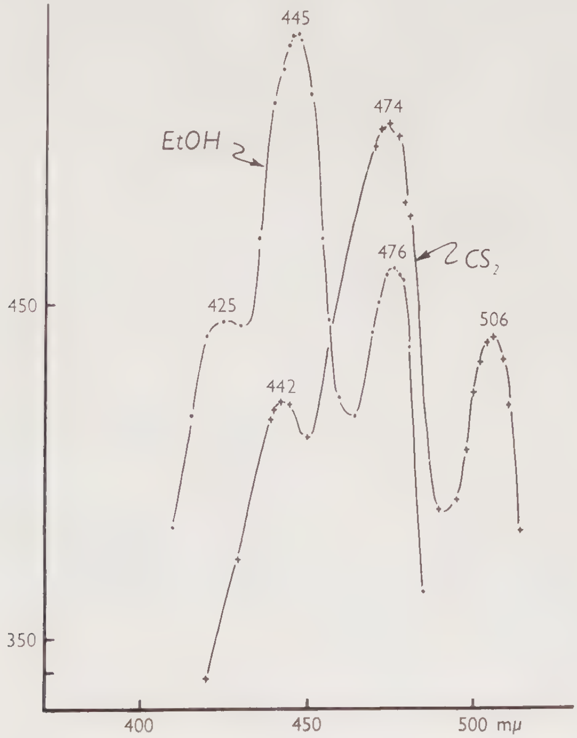


Fig. 3. Absorption spectra of diadinoxanthin from *Isochrysis* in ethanol and carbon disulphide.

the same pigment (Fig. 3). The lower maxima may indicate an imperfect separation from diadinoxanthin, though this was not shown by rechromatographing.

As far as the hypophasic fraction is concerned the main variation is in the presence of an additional band beneath the diadinoxanthin. From its position this might be diatoxanthin. Its colour was, however, similar to the band above, and when in measurable quantity had a maximum around 446 mμ in ethanol. It was found in 167, 168 and 93, but not in the others.

The epiphase is far more variable in quantity and is invariably less than the quantity of xanthophylls. In some the carotenes represent only a small part of the total carotenoid content. Alumina columns were not always effective in separating the carotenes, but both α- and β-carotenes were present in all, as shown by subsequent separation on magnesium oxide. In 147 there was almost as much α- as β-carotene, though there was little of either as compared with the quantity of xanthophylls.

DISCUSSION

No water-soluble pigments have been found and presumably Gaidukov's (1900) extracts were contaminated. The presence of fucoxanthin reported by Carter *et al.* (1939) is confirmed, and the additional evidence that the lutein-like pigment is diadinoxanthin is interesting in view of the relationship of the Chrysophyceae with the Bacillariophyceae in which this latter pigment is also to be found (Strain *et al.* 1944). The identification of chlorophyll *a* alone confirms the findings of Seybold *et al.* (1941). In view of recent work on the pigments of the Xanthophyceae or Heterokontae (Strain, 1958) in which the xanthophylls are certainly neither fucoxanthin nor diadinoxanthin, it would seem that the Chrysophyceae are not nearly related to them and that Pascher's 'Chrysophyta' is unnatural. The main difference between the diatoms and the Chrysophyceae as far as the pigments are concerned is the apparent absence of chlorophyll *c* and diatoxanthin in the latter. This is interesting in relation to the recent discussion of the taxonomic position of *Phaeodactylum* which in some ways seems intermediate in position between the two groups. Lewin, Lewin & Philpott (1958) have recently put forward evidence that *Phaeodactylum* belongs to the diatoms and the presence of chlorophyll *c* confirms this. On the other hand it is more like the Chrysophyceae in having fucoxanthin and diadinoxanthin but no diatoxanthin (Gilchrist & Green, 1960). A detailed re-examination of the pigments of particular members of both the Bacillariophyceae and the Chrysophyceae might prove a rewarding study for the elucidation of their relationship.

The predominantly golden colour of the Chrysophyceae is presumably due to the relatively large quantity of carotenoids of which the greater part are xanthophylls.

I am most grateful to Dr M. Parke for culturing the algae for me at the Plymouth Laboratory, and I also wish to thank Dr B. M. Gilchrist of Bedford College for kindly providing the cultures of *Phaeodactylum* and *Dunaliella*.

SUMMARY

No special pigments have been found in any of the marine Chrysophyceae examined. In all species the only chlorophyll identified was chlorophyll *a*. The carotenes represent a much smaller part of the total carotenoids than the xanthophylls, and the amount varies greatly from one species to another, perhaps accounting for their variable colour. α-Carotene represents a large proportion of the carotenes; γ-carotene was identified only in *Isochrysis galbana*. Fucoxanthin and diadinoxanthin represent the main xanthophylls.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

Atkins, D., 1959. The growth stages of the lophophore and loop of the brachiopod *Terebratalia transversa* (Sowerby). *J. Morph.*, Vol. 105, pp. 401–26.

The growth stages of the lophophore and loop from the early schizolophe to the adult plectolophe are described for the first time. The descending branches of the loop grow from both crura and septum to meet and fuse; the bearing of this on the taxonomic position of the species is discussed. Characteristic of the early growth stages is the presence of conspicuous flanges on the hood: these gradually become reduced in size and disappear about the time the ascending branches become free from the septum. The flanges are compared with accessory brachial structures in other terebratellaceans. The structure of the adult lophophore is described. The ciliary feeding mechanism is essentially similar to that already described by the author in other brachiopods with plectolophous lophophores.

D. A.

Bone, Q., 1959. The central nervous system in larval acraniates. *Quart. J. micr. Sci.*, Vol. 100, pp. 509–27.

A part of the organization of the spinal cord of acraniate larvae is described, chief attention being directed toward those tracts and cell groups which are probably concerned with the control of the swimming pattern. The first section deals with the arrangement of the fibre tracts in the cord, and of the cell bodies giving rise to these fibres. The form and connexions of the giant Rohde cells are then described, it is shown that these cells possess peripheral processes passing out of the dorsal root nerves, and are thus similar to the Rohon-Beard cells of craniate embryos. It is concluded that at present, it is not safe to homologize these two cell types, for the acraniate Rohde cells differ in several respects from the craniate Rohon-Beard cells. The innervation of the gill musculature is described, it is shown that it is asymmetrical, and that this asymmetry is not related to changes in symmetry at metamorphosis.

Finally, the arrangement of the whole system is discussed in relation to the systems found in the larval stages of primitive craniates.

Q. B.

Carlisle, D. B., 1960. Sexual differentiation in Crustacea Malacostraca. *Mem. Soc. Endocrin.*, Vol. 7, pp. 9–15.

A summary of the present state of our knowledge of the endocrine control of sexual differentiation in the higher Crustacea, drawing attention to the role of the vas deferens gland and the X organ–sinus gland complex. The paper includes a classification and terminology of the various types of successive hermaphroditism.

D. B. C.

Jewell, B. R., 1959. The nature of the phasic and the tonic responses of the anterior byssal retractor muscle of *Mytilus*. *J. Physiol.*, Vol. 149, pp. 154–77.

In this paper a further attempt has been made to elucidate the nature of the phasic and the tonic responses that are produced by many lamellibranch muscles. Experiments involving release techniques have shown that two quite distinct states of contraction are possible in the anterior byssal retractor muscle of *Mytilus*: there is an 'active' state which bears a strong qualitative resemblance to that found in vertebrate skeletal muscle, and a 'fused' state which appears to be peculiar to lamellibranch muscle in that it allows considerable tensions to be maintained with a very low expenditure of energy. A theory has been put forward in which it is postulated that all types of excitatory stimuli produce an 'active' state which gives way to a 'fused' state when stimulation ceases, and it is supposed that inhibitory stimuli act by abolishing the 'fused' state. By means of this hypothesis it is possible to explain many of the curious properties that are characteristic of lamellibranch muscle. B. R. J.

JONES, W. C., 1959. Spicule growth rates in *Leucosolenia variabilis*. *Quart. J. micr. Sci.*, Vol. 100, pp. 557–70.

The growth of triradiate spicules was investigated by photographing at intervals three pieces of the wall of the oscular tubes. The basal rays grew faster than the paired rays at first, but for both types of ray the growth rate increased to a steady level as the rays lengthened. When their length exceeded 25 μ, the basal and paired rays grew at similar rates, regardless of the different relationships between the axis of the rays and the orientation of the optic axis of the mineral constituent. The average rates for rays exceeding 25 μ on the three pieces were respectively 2·50 (18–21° C), 1·64 (18° C) and 1·29 (17° C) μ per hour. W. C. J.

NICHOLS, D., 1959. The histology and activities of the tube-feet of *Echinocyamus pusillus*. *Quart. J. micr. Sci.*, Vol. 100, pp. 539–55.

The histological structure of the tube-feet of this clypeasteroid sea-urchin is interpreted functionally. Each suckered tube-foot possesses a special set of levator muscles within its lumen to raise the centre of the disk for attachment. The disk is probably raised further by contraction of a ring of short muscles embedded in the disk itself; these muscles are also active in detachment, pulling the edge of the disk away from the substratum relative to the disk centre. There are four columns of retractor muscles in the tube-foot stem for postural movement. The buccal sensory tube-feet have a ring of cilia, probably tactile, round the edge of the disc and a nervous pad, probably chemoreceptive, in its centre. Circulation of oxygenated water round the respiratory tube-feet is maintained by patches of external cilia and the tall thin shape is maintained by cross-connexion internally. D. N.

WELLS, G. P., 1960. The genera of Arenicolidae (Polychaeta). *Proc. zool. Soc. Lond.*, Vol. 133, pp. 301–14.

It is argued that the species currently grouped as *Arenicola* Lamarck should be distributed between *Arenicola*, *Arenicolides* Mesnil and *Abarenicola* gen.nov. Formal diagnoses of the family and its constituent genera are given and suggestions are made as to the most convenient characters for referring arenicolid worms to their genera. The forms found at Plymouth are *Arenicola marina*, *Arenicolides ecaudata* and *Arenicolides branchialis*. G. P. W.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1959–60

The Association was greatly honoured on 18 March 1960 by a visit to the Plymouth laboratory of our Patron, H.R.H. The Duke of Edinburgh. His Royal Highness spent over an hour in the laboratory and aquarium, and met members of the staff and visiting research workers. The President and Honorary Treasurer were present for the occasion.

The Council have to report with regret the death of Dr W. R. G. Atkins, C.B.E., F.R.S., who was Head of the Department of General Physiology at the Plymouth laboratory from 1921 to 1955. During these years Dr Atkins laid the foundations of much of our present knowledge of the chemistry and physics of the sea and brought international renown to the Plymouth laboratory.

THE COUNCIL AND OFFICERS

Four ordinary meetings of the Council were held during the year, two in the rooms of the Royal Society, one in the rooms of the Linnean Society and one at Plymouth. At these the average attendance was eighteen.

THE PLYMOUTH LABORATORY

During the year a small wooden building was erected on the reservoir roof in the space between the lavatories and the porch of the door into the north building. This is to house subaqua diving equipment, which is now much in use. Two windows have been enlarged and a new window built in the lavatories.

The internal decoration of the south building has been completed, and the outside woodwork and chuting of the north wall repaired and repainted.

LABORATORY EXTENSION

The Council are pleased to report that H.M. Treasury have sanctioned a grant to meet the cost of an extension to the Plymouth laboratory. The north building will be extended and consist of cellars for experimental work, physiological laboratories on the ground floor, and chemical laboratories on the first floor. The north and south buildings will be joined by an extension having a lecture hall on the ground floor and botanical laboratories on the first floor. It is hoped that building will begin at the end of April 1960.

AQUARIUM

The new aquarium was officially opened on 30 June 1959 by the Lord Mayor of Plymouth, Councillor P. N. Washbourn, who cut a strand of sea-weed with a pair of silver grape scissors presented by the Architects.

The aquarium was designed by our architect, Mr F. L. Preston, F.R.I.B.A., of Messrs Easton & Robertson, Cusdin, Preston and Smith, London, from original plans and ideas supplied by Dr D. P. Wilson. It was built by Messrs John Garrett & Son, Ltd., Builders, of Plymouth, and the rockwork was designed and carried out by Mr H. R. Allen, A.R.C.A., of Westerham. The whole construction has been most successful and is much appreciated by the public.

The new aquarium differs radically from the old, is pleasingly proportioned and much better lit. Quietness is ensured by an acoustically tiled ceiling. Tanks extend part-way along both north and south walls, somewhat as before, but they are of equal depth from back to front so that the row of pillars supporting the floor above is now centrally placed. A very large tank at the east end occupies the whole width of the room, with alcoves between it and the eastern ends of the north and south rows of tanks. The north alcove contains one small tank and the south alcove a small tank and an emergency exit. As viewed from the public entrance the three windows of the big tank complete an attractive vista.

The new tanks, of which there are eighteen, vary in size from very large to very small. With the exception of the three smallest none is rectangular, side walls being set at 45° so that tanks wider behind than in front alternate with triangular tanks. This is the arrangement first suggested by J. Garnaud in 1952 and subsequently carried out in the aquarium of the Institute of Oceanography at Monaco. The tanks are of reinforced concrete with slate inserts framing the window openings, which are mostly a foot wider than in the old aquarium. Lintel walk-ways and catwalks above the tanks hidden from public view greatly facilitate servicing. The sea water mains are of black polythene and the flow is regulated with 'Saunders' diaphragm valves with polythene bodies. Inflowing water enters the tanks at concealed positions and emerges at the bottom. Overflow pipes of asbestos are cast in the thickness of the walls and drain off surface water. Compressed air is used to increase water movement within the larger tanks and to give a rippled surface with resulting pleasing play of light and shadow over the bottom. Removable partitions between the largest tanks will allow fish to be diverted from one tank to another during major cleaning operations. Electric lighting is used, and almost all daylight is excluded. There are special arrangements for ventilating the public hall. These are but few of the new features which will be described in detail in a future number of the *Journal*.

The Council wish to record their appreciation of the very valuable assistance given by Dr D. P. Wilson who spent so much time and thought in seeing the work through to completion from his original ideas. The Council also wish to thank those members of the Plymouth laboratory staff who gave special technical assistance, especially Mr A. N. Bennett, Mr F. G. C. Ryder and Mr F. J. Warren.

RESEARCH SHIPS

Apart from normal overhauls the three research vessels R.V. 'Sarsia', R.V. 'Sula' and M.V. 'Gammarus' have operated regularly throughout the year.

RAY LANKESTER INVESTIGATOR

The Council have pleasure in reporting that Prof. J. E. Smith, F.R.S., has been appointed Ray Lankester Investigator to work at the Plymouth laboratory in 1960.

GRANT FOR FLAGELLATE RESEARCH

The Council are pleased to report that H.M. Treasury have sanctioned a grant to the Association to enable a cytologist to assist in the research on marine flagellates with the electron microscope which is being done in Prof. Irene Manton's department at Leeds University in collaboration with Dr Mary Parke. Dr G. F. Leedale has been appointed for this purpose as from 1 October 1959 and seconded to work at Leeds.

STAFF

Mr J. V. Howarth joined the staff of the Plymouth laboratory as Senior Scientific Officer on 1 April 1959.

Dr L. H. N. Cooper attended the International Oceanographic Congress in New York in September 1959 and the meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1959.

Dr Mary Parke attended the Ninth International Congress of Botany in Montreal in August 1959 and the International Oceanographic Congress in New York in September 1959.

Dr E. J. Denton attended the International Oceanographic Congress in New York in September 1959.

Dr D. B. Carlisle worked during September 1959 at the Kristinebergs Zoologisk Station in Sweden and attended the meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1959.

Dr T. I. Shaw and Dr G. W. Bryan attended the Meeting of the International Atomic Energy Agency and U.N.E.S.C.O. Conference on the Disposal of Radioactive Wastes held in Monaco in November 1959.

OCCUPATION OF TABLES

The following one hundred and forty-one workers have occupied tables at the Plymouth Laboratory during the year.

Miss M. N. E. ADAMS, Kingston-upon-Thames (Library).
E. ADAMS, Plymouth (Library).
Dr J. S. ALEXANDROWICZ, Plymouth (Nervous system of invertebrates).
S. R. ARMSTRONG, Bryanston (Molluscs).
D. C. ARNOLD, Swansea (Library).
Dr DAPHNE ATKINS, Plymouth (Brachiopods).
W. J. BALLANTINE, D.S.I.R., London (Ecology of limpets).
Dr P. R. O. BARNETT, Southampton and Millport (Bottom copepods).
Prof. E. J. W. BARRINGTON, Nottingham (Histochemistry of *Amphioxus* and tunicates).
E. R. B. BERNABE, Manila (Plankton).
Dr ANNA M. BIDDER, Cambridge (Cranchid histology).
Dr G. T. BOALCH, International Paints Research Fellow (Effects of toxic substances on algae).
Dr A. D. BONEY, Plymouth (Ecology of red algae).
J. BRACKEN, Dublin (S. Ireland herring fishery).
M. C. BROWN, London (Library).
Dr ELEANOR M. BROWN, London (Plankton).
Dr P. C. J. BRUNET, Oxford (Biochemistry of dogfish egg-capsule).
Prof. W. D. BURBANCK, Woods Hole (Ecology of *Cyathura*).
A. C. BURD, Lowestoft (S. Ireland herring fishery).
B. M. H. BUSH, Cambridge (Crustacean neuro-muscular physiology).
Miss J. G. CALDWELL, Yale (Crustacea).
Dr P. C. CALDWELL, Alan Johnston, Lawrence and Mosely Research Fellow of the Royal Society (Muscle and nerve physiology).
Dr PHOEBE CALDWELL, Plymouth (Library).
Dr M. R. CLARKE, N.I.O. Wormley (Testing otter boards).
Miss E. CLAY, Brixham (Library).
J. W. COLES, London (Shore collecting).
D. A. CONROY, Berkhamsted (Library).
C. A. COSWAY, Torquay (Library).
Miss A. C. COUPLAND, Birmingham (Trematode parasites).
Dr C. B. COWEY, Shinfield (Vitamin B_{12} in sea water).
J. W. COWIE, Bristol (Submarine geology).
W. D. G. COX, Chichester (Library).
Dr A. B. CRIBB, Brisbane (Algal taxonomy and ecology).
Dr D. J. CRISP, Anglesey (General).
D. CURRY, Bristol (Submarine geology).
Dr K. W. DAISLEY, Shinfield (Vitamin B_{12} in sea water).
Dr R. PHILLIPS DALES, London (*Spirographis*).
Mrs M. PHILLIPS DALES, London (*Spirographis*).
F. W. DARWIN, Cambridge (Gastropod osphradia).
Dr G. B. DAVID, Cardiff (Library).
J. B. DAVIES, Oxford (General).
Dr ELIZABETH J. DIMELOW, New Brunswick (Biology of *Antedon*).
L. A. W. DOWNER, Tavistock (Library).
J. H. ELGOOD, Rustington (Library).

D. J. ELLETT, Lowestoft (S. Ireland herring fishery).
Mrs JOY ETHERINGTON, London (*Ectocarpus*).
D. ETHERINGTON, London (*Phascolion*).
Dr L. R. FISHER, Shinfield (Pigments of invertebrate eyes).
I. H. FORD, Bristol (Submarine geology).
Mrs J. D. FREEMAN, London (Digenetic trematodes).
R. F. H. FREEMAN, London (Metabolism of *Scrobicularia*).
DR VERA FRETTER, Reading (Prosobranch molluscs).
Dr I. FRIEDMANN, Leeds (Ecology of *Prasicola stipitata*).
Prof. A. C. GIESE, U.S.A. (Constituents of tissues of echinoderms).
K. R. GILL, Cambridge (Magnetic survey of W. Approaches).
Dr J. B. GILPIN-BROWN, Plymouth (Biology of nereids; cuttlefish).
D. R. GLASSON, Cambridge (Magnetic survey of W. Approaches).
Dr I. M. GOODBODY, Jamaica (Digestion in ascidians).
Prof. A. GRAHAM, Reading (Prosobranch molluscs).
P. J. M. GREENDALE, Exeter (Library).
D. N. F. HALL, Colonial Office (Indo-west Pacific Penaeidae).
Dr Y. HANEDA, Yokosuka (Bioluminescence).
EIJI HARADA, Kyoto (Crustacean larvae).
M. G. HARDY, Reading (Histology of lamellibranchs).
Prof. J. E. HARRIS, F.R.S., Bristol (Vertical migration of plankton).
J. W. HARRISON, Cambridge (Magnetic survey of W. Approaches).
Dr H. W. HARVEY, F.R.S., Plymouth (Productivity of sea water).
B. T. HEPPER, Conway (Lobster marking).
Dr M. N. HILL, Cambridge (Magnetic survey of W. Approaches).
Dr J. A. HINKE, London (Squid axons).
Prof. A. L. HODGKIN, F.R.S., Cambridge (Physiology of squid giant axons).
Dr G. M. HUGHES, Cambridge (Gill structure of fishes).
D. J. HUME, Teignmouth (Library).
O. D. HUNT, Newton Ferrers (Library).
B. L. JAMES, Aberystwyth (Trematode parasites of gastropods).
Dr C. H. JELLARD, Plymouth (Library).
Dr PENELOPE M. JENKIN, Bristol (Library).
Dr N. G. JERLOV, Göteborg (Light penetration in sea).
Dr G. Y. KENNEDY, Sheffield (Chlorophyll pigments).
Dr A. K. KENT, London (Teleost colour changes).
Mrs R. S. M. KENT, London (Uptake of 'thoroplast').
Dr R. D. KEYNES, F.R.S., Cambridge (Physiology of squid giant axons).
Dr H. G. KLEMPERER, London (Iodine metabolism of algae).
Sir FRANCIS G. W. KNOWLES, Birmingham (Crustacean endocrinology).
Dr S. K. KON, Shinfield (Pigment of invertebrate eyes).
Dr S. KRISHNASWAMY, Southampton (Fat content of plankton).
Dr MARIE V. LEBOUR, Plymouth (Decapod larvae).
J. G. E. LEWIS, London (Distribution and reproduction of *Scolioplanes*).
Dr J. LLEWELLYN, Birmingham (Trematode parasites of fishes).
Miss R. D. LONG, Plymouth (Library).
Prof. O. E. LOWENSTEIN, F.R.S., Birmingham (Central nervous responses in elasmobranchs).
M. J. MANN, Lagos (Library).
Prof. IRENE MANTON, Leeds (Library).
Dr SHEINA M. MARSHALL, Millport (Respiration of *Calanus*).

A. L. Martin, London (Library).
M. H. Martin, Looe (Library).
Miss H. F. Maunsell, D.S.I.R., Oxford (Crustacean endocrines).
R. Mayne, Plymouth (Library).
Dr Frances M. Molloy, Rothamsted (Digestion in mysids).
Dr J. E. Morton, London (Molluscs).
Dr R. W. Murray, Birmingham (Neurophysiology and body fluids of elasmobranchs).
H. Mutvei, Stockholm (Molluscs).
Prof. G. E. Newell, London (Library).
Dr D. Nichols, Oxford (Histology of holothurians).
A. M. Olsen, Hobart (Library).
Dr A. P. Orr, Millport (Respiration of *Calanus*).
K. H. Palmork, Bergen (Chemistry of sea water).
Dr K. Pampapathi-Rao, India (Sensory physiology of rays).
Prof. C. F. A. Pantin, F.R.S., Cambridge (*Hydratuba*).
C. J. Pennycuick, Cambridge (Physiology of dogfish locomotion).
Dr W. T. W. Potts, Birmingham (Body fluids of elasmobranchs).
B. L. Powell, Swansea (*Carcinus* endocrine organs).
Cdr. C. F. B. Powell, R.N. (Rtd.), Plymouth (Library).
M. Quick, Bristol (Submarine geology).
A. M. Qureshy, London (Haemogregarines of fishes).
Prof. J. E. G. Raymont, Southampton (Fat content in marine plankton).
Dr W. J. Rees, British Museum (*Stygiomedusa*).
D. J. Rowlands, London (General).
D. J. Scarratt, D.S.I.R. (Fauna of *Laminaria* holdfasts).
Miss J. M. Shephard, London (Polyzoa).
J. Shields, Southampton (Effects of metals upon marine organisms).
Prof. J. E. Smith, F.R.S., Ray Lankester Investigator, London (Nervous system of *Echinus*).
Dr Eve C. Southward, Plymouth (Pogonophora; polychaetes).
B. W. P. Sparrow, Newton Ferrers (Library).
Miss F. A. Stanbury, Plymouth (*Cladophora*).
O. Suddaby, Plymouth (Library).
Dr Muriel F. Sutton, London (Ascidians).
M. E. U. Taylor, Lowestoft (S. Ireland herring fishery).
Dr K. K. Tiwari, Calcutta (General).
R. Vaissière, Algiers (Deep-water copepods).
Dr H. G. Vevers, London (General).
Miss J. D. Waddle, London (General).
G. E. Walster, Plymouth (Glycolysis in *Maia*).
Miss B. V. Warne, Stafford (General).
Prof. T. H. Waterman, Yale (Crustacean physiology).
Dr J. O. Wersäll, Stockholm (Innervation of hair cells of elasmobranchs).
Prof. W. F. Whittard, F.R.S., Bristol (Submarine geology).
J. H. Wickstead, Colonial Office (Tropical plankton).
Dr H. H. Williams, Aberystwyth (Helminth parasites of elasmobranchs).
Dr S. E. Wilson, London (Feeding habits of *Teredo*).
R. C. Woledge, London (Muscle physiology).

Among the many other scientists who have visited Plymouth during the year to see the general work of the laboratory and to discuss problems with members of the scientific staff, the following have come from overseas: Prof. S. D. Gerking (U.S.A.), D. E. Kurth (Australia), Miss B. A. Lewis (Pakistan), Dr Howard S. Mason (U.S.A.), Dr M. J. Cohen (U.S.A.), J. Hamre (Bergen), Dr I. D. Hiscock (Queensland), Dr Chas. C. Davis (U.S.A.), Dr Mary A. Pocock (S. Africa), Dr M. M. Vaskesaeger (Belgium), Dr L. P. Sayles (U.S.A.), Dr D. S. Rawson (Canada), Prof. F. Crescitelli (U.S.A.), Dr S. Uyeda (Japan), J. Phipps (Sierra Leone), Prof. A. von Muralt (Switzerland), Dr A. M. Shanes (U.S.A.), Prof. F. A. Brown (U.S.A.), Prof. M. Uda (Japan), Dr W. Wieser (Austria), Dr A. J. Kohn (U.S.A.), Miss P. McDonald (Sydney), Dr G. M. Moore (U.S.A.), Dr D. Davenport (U.S.A.), Prof. A. Barash (Israel), Nezihe Öztan (Turkey), P. de Wolf (Holland), Prof. A. Fleckenstein (Germany), B. Carlburg (Sweden), M. Waldichuk (Canada), Prof. E. R. Noble (U.S.A.), Prof. G. A. Knox (New Zealand), A. A. Mills (Canada), Dr G. F. Humphrey (Australia).

On 8 and 9 May a meeting of members of the Photobiology Group was held at the Plymouth laboratory. Papers were given by members of the staff and fourteen members of the group came to the laboratory for the meeting.

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin and were attended by thirty-nine students from the following Universities: Oxford, Cambridge, Reading, Exeter, Aberystwyth, Southampton, London, Sheffield, Glasgow, Swansea, Leicester, Durham, Newcastle, Cambridge Technical College and Regent Street Polytechnic.

Also during the Easter Vacation Mr J. Peirson brought a party of three boys from Rugby School and during the Summer Vacation Miss M. Christianson brought a party of six girls from Harrow County Girls' School.

SCIENTIFIC WORK OF THE PLYMOUTH LABORATORY STAFF

Sea Water and Plankton

The I.G.Y. cruise in November 1958, to the Gulf of Gibraltar by R.R.S. 'Discovery II', was staffed by an international team of nine scientists including Dr L. H. N. Cooper and Mr E. I. Butler from the Plymouth Laboratory. The purpose was to study in detail the manner of the outflow of the Mediterranean water and of its admixture with North Atlantic water. In addition to temperature measurements, more than 5000 chemical analyses on samples drawn from a grid of over 100 stations were made, followed at once by dynamic calculations. With this knowledge and with a chart of the echo-soundings obtained it was possible to place neutral buoyancy floats in positions where they could yield information of maximum value. Four laboratories are involved and working up is not complete. The most striking feature was a large eddy at 1250 m in the mixed Mediterranean–Atlantic water. The deep phosphate measurements combined with those of U.S.S. 'Crawford' promise evidence about the deep circulation. The cruise provided an opportunity to compare equipment and methods, particularly for oxygen determinations. Three standards on board for standardising thiosulphate did not give similar results. The issue was referred to Mr F. A. J. Armstrong who was able to show that dichromate, as used in one of the methods, is an unsatisfactory standard.

At the International Oceanographic Congress in New York Dr Cooper presented a paper based on work on R.V. 'Sarsia' and R.R.S. 'Discovery II' in 1958 in the northern Bay of Biscay in association with the I.G.Y. The main, but tentative, conclusion was that the deep ocean is filled not by water of steadily increasing density but by a series of strata, each of which is in neutral adiabatic equilibrium. Separating these 'resident water masses', there seem to be thin discontinuity layers within which density increases rapidly. These discontinuity layers, thin though they are, seem to have a strongly laminated structure, attributed to their possible origin as extension plates derived from boluses which have descended along the eastern face of the Reykjanes Ridge from the Iceland–Faeroe Ridge. Some consequences of this structure were presented.

He has also worked up the hydrographical observations made in the Celtic Sea in 1950 by R.V. 'Sir Lancelot', R.V. 'Sabella' and R.R.S. 'Discovery II'. Once the summer thermocline has been strongly developed, it seems that recruitment of new water into the English Channel comes only from thermocline level (25–45 m) west of Ushant. The waters from above and below the thermocline did not enter the Channel, neither in high summer did water from the westward. This agrees with Dr F. S. Russell's earlier deductions from biological indicators. This mechanism explains about one-half the loss in phosphate which water undergoes on passage from the Bay of Biscay into the English Channel. A more detailed understanding of the movement and nature of the waters in the Northern Celtic Sea and Bristol Channel has also been achieved.

Dr T. I. Shaw has started some experimental studies upon the state of iodine in sea water in order to examine the hypothesis put forward by him and Dr L. H. N. Cooper (*Nature*, *Lond*., Vol. 180, p. 250) that the oxidized form of iodine in sea water is hypoiodous acid rather than iodate. Preliminary results show that only a part of any carrier-free ^{131}I, added as iodide to sea water, is precipitable by silver ions; the addition of inactive iodate does not affect the amount of precipitable activity but the addition of either inactive iodide or a reducing agent such as sulphite render almost all the activity precipitable. These observations confirm that part of the iodine in sea water is in an oxidized form and indicate that this form, unlike iodate, is capable of rapidly exchanging its iodine atom with iodide.

Mr F. A. J. Armstrong and Mr E. I. Butler have continued the monthly cruises to the International Hydrographic Station E1. The results of analyses in 1958 have been prepared for publication in the *Journal*. In 1959 the monthly observations have been supplemented by two surveys (in January and in June) of the area surrounding the station, in an attempt to discover the immediate causes of the rather sudden changes which occur from time to time at E 1. In January some quite marked boundaries were found, near E 1, which was seen to be in the narrow part of a tongue of low salinity water of high phosphate and silicate content, which projected from Plymouth in a south-east direction for at least 50 miles into the Channel. In June, no such tongue was seen, but there was an interesting gradation from west to east with falling surface temperature and rising thermocline as vertical mixing increased. On neither occasion could it be said that conditions at E 1 were typical of the area off Plymouth.

In association with Dr G. T. Boalch, International Paints Research Fellow, Mr Armstrong has made measurements of the ultra-violet absorption of sea water samples. Small but significant increases in the 200–250 mμ region have been found in the spring, but the large absorption of the inorganic salts in this region makes the work difficult. During attempts to accentuate small differences by concentrating the water it was found that when sea water is distilled the distillate has a higher ultra violet absorption than has pure distilled water. The first 10% may have an absorbancy of 0·1–0·4 in a 10 cm cuvette at 200 mμ, and has a marked 'weedy' smell. There appears to be a seasonal variation with maximum values in late summer. The nature of this volatile material is not yet known. The weedy odour suggested the presence of dimethyl sulphide (which is known to be evolved by *Polysiphonia* and *Enteromorpha*) and in fact organic sulphides have been detected in those distillates from sea water, in quantities equivalent to about 1 μg S per litre. There is reason to associate these sulphides with the phytoplankton and indeed they have been found in considerably larger amount in a culture of *Phaeodactylum*. However, they can account for only a very small fraction of the volatile material.

With the co-operation of Mr E. I. Butler monthly samples of sea water have been taken again this year at stations L2–L6 and E 1 (surface to 70 m) for the examination of the nanoplankton by Dr Mary Parke and Miss I. M. Adams. The records of the organisms developing in temporary cultures set up from these samples now cover a period of 2 years and they are being tabulated to assess the information obtained by this study. A number of new interesting forms have been isolated during the year from these samples including an organism which so far cannot be placed with certainty in any algal class. Prof. I. Manton (electron microscopy), Dr G. Y. Kennedy (pigments), Dr M. R. Droop (growth requirements) and Mr J. Dodge (cytology) are co-operating in the study of this organism.

Valuable information is also being accumulated by Dr Parke and Miss Adams on the life histories of a number of organisms in the Plymouth collection. It is now known that the recently described coccolithophorid

Crystallolithus hyalinus, two strains of which were successfully isolated last year and which is similar to the genus *Chrysochromulina*, except that it has a deposit of calcite crystals on its scales, is the motile stage in the life history of the well-known non-motile coccolithophorid *Coccolithus pelagicus*. This finding is of extreme importance from the point of view of the classification of the Coccolithophoridaceae. The system of classification developed recently in which two main series are separated, i.e. organisms bearing holococcoliths and organisms bearing heterococcoliths, will have to be abandoned, since both types (holococcoliths on *Crystallolithus hyalinus* and heterococcoliths on *Coccolithus pelagicus*) can be found on different stages in the life history of one organism. Another organism of the *Crystallolithus* type, probably the motile stage of another well-known coccolithophorid, has just been isolated for the study of its non-motile phases.

It has also been found that the organism *Pleurochrysis scherffelii* must be placed in the Coccolithophoridaceae since both motile and non-motile stages become covered by coccoliths and the motile stage bears, in addition to two acronematic flagella, a very short haptonema.

Knowledge concerning the problematic genus *Ochrosphaera* has also been considerably increased during the past year. Previously it was considered to have an *Ochromonas*-type motile stage, but it has now been shown that the motile stage of the type species, *O. neapolitana*, is covered by scales and has two acronematic flagella as do other motile coccolithophorid stages. Interesting cyst stages of this organism have also developed in culture, the structure of which may help in the understanding of some recent and fossil cyst forms placed in the families Thoracosphaeridae and Discoasteridae as the organisms which produced them were unknown. Recently Mr W. J. Ballantine of Queen Mary College, London, drew our attention to a brown symbiont in the ciliate *Urceolaria patellae* (Cuénot) living on the pallial gills of *Patella aspera*. By culturing the symbiont it has been shown to be a stage in the life history of an *Ochrosphaera* species, probably *O. neapolitana*.

Work has also continued on the isolation and culturing of *Phaeocystis* type colonies and it has now been proved that the commonly occurring *P. pouchetii* has two types of motile phase, structurally different, in its life history. Cultures of *Phaeocystis* colonies have also been sent to Prof. J. McN. Sieburth of the Department of Veterinary Science, Virginia Polytechnic Institute, U.S.A., to be used in connexion with his work on antibacterial activity in the gastro-intestinal tract of penguins, since the activity is thought to be caused by *Phaeocystis*.

Dr F. S. Russell has continued the preparation of a monograph on British scyphomedusae. He has now completed the Coronatae, of which seven species are known to occur in deep water west of the British Isles. On a cruise in October 1959 to the Bay of Biscay R.V. 'Sarsia' collected a very large deep-sea scyphomedusa in a deep-water haul off Santander. This has proved to be a new genus and species and Dr Russell has published a preliminary note in *Nature* giving the medusa the name *Stygiomedusa fabulosa*. The most striking feature is that it is viviparous. The medusa, which is about 50 cm in diameter, has attached capsules from which perfectly developed young hatch which are already about 10 cm in diameter. A detailed description is being prepared in collaboration with Dr W. J. Rees of the British Museum (Nat. Hist.).

Dr E. D. S. Corner has begun an investigation of the nutrition of the copepod *Calanus helgolandicus*. An apparatus has been constructed in which up to 300 animals can be kept for several days under a continuous flow of 'outside' sea water; and the quantities of food which they remove has been estimated from analyses of the changing amounts of suspended organic matter in the medium. Initial experiments have shown that the quantities of carbohydrates, protein and fat assimilated daily by the animals from 'outside' sea water are more than enough to account for their respiration rate. However, *Calanus* kept under these conditions showed no increase in weight, nor were they able to survive for more than 5–6 days. Accordingly, further experiments are planned in which the animals will be allowed to feed in sea water to which varying amounts of different species of diatoms have been added.

Dr A. J. Southward has continued investigations on the distribution of zooplankton 'indicator' species in the western Channel by means of high-speed samplers. The area surveyed has been extended to include parts of the Bristol Channel and north Celtic Sea in order to study macroplankton resembling that found off Plymouth before 1930. Samples taken by the research vessels 'Sir Lancelot' and 'Anton Dohrn' have been examined as well as standard ring trawl hauls taken in earlier years by R.V. 'Sarsia'. A preliminary account of the work is being prepared and it is hoped to present an explanation of the faunistic and other changes that have taken place in the area since the 1900's.

Macro-fauna and Flora

Dr Parke has published 'Corrections and Additions III' to the 'Check-list of British Marine Algae' in the *British Phycological Bulletin*, No. 7.

The fine spring, summer and autumn of 1959, following a mild winter, has had marked effects on the abundance of intertidal barnacles. Dr A. J. Southward has found that the northern species, *Balanus balanoides*, has declined, the new generation having failed to settle or survive. In contrast, extensive early settlements of the southern form, *Chthamalus stellatus*, occurred at all stations examined, and the young specimens showed a high rate of growth. Work on cirral activity of barnacles has been continued: valuable ciné records of the large species, *Balanus hameri*, were obtained during a visit to the Marine Biological Station, Port Erin. In collaboration with Dr D. J. Crisp, Dr Southward has published a note, in Vol. 38, No. 3 of the *Journal*, on the further spread of the immigrant Australasian barnacle, *Elminius modestus*, in the British Isles, based on surveys made up to the spring of 1959. A joint account of recent changes in the distribution of marine organisms in north-west Europe was prepared for the International Oceanographic Congress in New York, where it was read by Dr Crisp.

Dr D. P. Wilson has prepared for publication in Vol. 38, No. 3, of the *Journal* an account of another new species of the polychaete genus *Magelona* and has named the new worm *filiformis*. It was first found in 1939 at Mill Bay, Salcombe, in silty sand near low-water mark associated with *M. papillicornis*. Although still fairly common it appears to be now less abundant than when first found. Fragile and extremely slender, it reaches a length of about 10 cm and is distinguishable from all other known species of the genus by the shape of its prostomium and by its parapodial characters. In its typical form it has been obtained only at Salcombe, but a markedly dwarf variety exists off shore off the east coast of Scotland. This dwarf form had been recorded by Mr A. D. McIntyre as *M. rosea* Moore. Dr Wilson has found, after examining specimens kindly sent by Mr McIntyre, that it is not only not *rosea* but that it is structurally identical with *filiformis* from Salcombe, although very much smaller when adult. After seeing Salcombe specimens Mr McIntyre is in agreement with this. In his paper Dr Wilson compares *filiformis* with other species of *Magelona*, especially *longicornis* Johnson which is shown to be imperfectly established, and with *cornuta* Wesenberg-Lund the original account of which he has amended and expanded from a re-examination of the type specimen.

Mr G. M. Spooner has continued the study of the fauna of the Eddystone shell-gravel and comparable deposits, and is attempting to distinguish between the members living close to the surface and those distributed through the bulk of the deposit. The Forster anchor-dredge is proving useful for this purpose.

Among additional small malacostracans found in the Eddystone gravel are two further representatives of phreatic genera of special interest. One is a new species of *Ingolfiella* itself, an isolated amphipod genus which, though very seldom observed, is already noted for its remarkable cosmopolitan distribution. Twenty specimens have now been isolated from the only two hauls made with the anchor-dredge. The other is a new species of the genus *Bogidiella*, the first truly marine species to be discovered. The genus, to date, is known from southern Europe and Asia and South America; six of the previously known species occur in terrestrial ground water, and three interstitially in intertidal deposits. In addition, further examples of a species (found first last year) belonging to a new genus of the Bogidiellidae have been found.

In a letter to *Nature* published in June 1959, certain other little-known animals are recorded, some of which had not previously been noticed in British waters. For example, three species of acochlideacean gastropods, representing three separate families, appeared in a bucket of gravel collected by Mr G. R. Forster near the entrance to the Sound. With these three species a new suborder can now be added to the list of British Mollusca. One of these species appears also in the Eddystone gravel, together with another that is probably identical with one quite recently described from the Kiel area.

The same letter also briefly points out the significance of the occurrence of species of phreatic genera in marine gravels. These animals may be considered as having invaded the gravels *from below* rather than from the water above—that is to say, the species, genera, or even families to which they belong have slowly spread and evolved in ground-water held by the rocks of the earth's crust, and have penetrated under continent and ocean alike.

A single specimen of another blind colourless crustacean, *Microjaera anisopoda*, originally described from two specimens taken off Roscoff, was found in the Eddystone gravel. Now about twenty specimens have been got from clean coarse sand in the Isles of Scilly—in the famous 'silver strand' of Tresco—in company with a subterrestrial fauna. This genus, therefore, may well be represented in fresh water.

The fauna of the Eddystone Rock is being studied and is showing features of interest. The fauna of arthropods and worms that seek shelter in the various tufted weeds, clumps of barnacle shells and cracks in the rock itself, is notably denser than on rocks along the coast of the mainland. Among amphipods *Parajassa pelagica* is abundant, while the genus *Hyale* is represented by three species which show overlapping ranges—*H. perieri* from the splash zone to near mid-tide level, *H. stebbingi* between low H.W.N. and high L.W.N., and *H. pontica* from somewhat below mid-tide to E.L.W.S. Insects are represented by at least three species—*Thalassomyia frauenfeldi* (larvae in the upper *Enteromorpha*), *Aphrosylus celtiber* (adults on wing and larvae in *Corallina*), and *Clunio marinus* (larvae in *Corallina*). The *Enteromorpha* carries a heavy population of marine mites of the genus *Metarhombognathus*.

Mr P. G. Corbin has continued to collect data on the Lucernarians and certain of the smaller fishes. An interesting record from the Scilly Isles was the find, in April 1959, of a single specimen of *Lucernaria quadricornis* by Mr J. M. Lock of Charterhouse School. This is a species not uncommon apparently in Norway, but the certain British records are only very few. Further notes have been made on the ventral melanophore patterns of small specimens of the three Dragonets, *Callionymus* spp. The Connemara Sucker, *Lepadogaster candollei*, recorded as rare in the second edition of the Plymouth Marine Fauna (1931) and not found in the area in the last 10 years although looked for intensively, has been found by the I.C.I. Marine Paints Division Laboratory, Brixham, to occur regularly at one beach in the neighbourhood. With a locality now known for the species, it is hoped to make further notes on its natural history.

Following the discovery of a form of the lamellibranch *Lutraria* corresponding to *L. elliptica* var. *angustior* Philippi, Mr N. A. Holme has made a study of the British species of this genus. In a paper published in Vol. 38, No. 3 of the *Journal* it is shown that this form differs sufficiently from *L. lutraria* (= *elliptica*), both in shell characters and in the form of the siphons, to merit specific rank. It has accordingly been called *L. angustior* Philippi, and the differences between it and the other two species described. Shells and siphons of *L. angustior* are regularly taken in dredgings from the Eddystone shell-gravel, and this species appears to be widely distributed in similar deposits elsewhere in the English Channel.

In Volume 38, No. 3 of the *Journal*, Mr N. A. Holme has described a hopper used at sea for washing bottom deposits into suspension, so facilitating sieving of dredge and grab hauls. This apparatus has been in use for a number of years, and has considerably reduced the labour involved in sieving large samples.

During the year Mr N. A. Holme has made a detailed qualitative survey of the bottom fauna of the English Channel. Samples have been taken with a heavy version of Forster's anchor-dredge at 147 stations off the south coast of England, mainly in depths of less than 25 fathoms. Study has centred on the distribution of lamellibranchs and echinoderms, and account has also been taken of empty shells as additional evidence of the absence of species from a particular area. While not directly comparable with the shore survey of D. J. Crisp and A. J. Southward published in Vol. 32, No. 1 of the *Journal*, the results agree in showing the absence of many species from the eastern basin, the most distinct boundary being in the region of Portland Bill, while other species reach their limit at the Isle of Wight. Comparison with data from the North Sea shows that certain species absent in the eastern basin occur in lower temperatures in the central and southern North Sea. This, and the absence of marked temperature gradients at the critical region between the east and west basins of the Channel, indicate that for some species temperature is not a direct limiting factor in the Channel.

Another, less well-defined, boundary lies somewhat to the west of Plymouth, and marks the eastward limit of certain species which may be associated with 'western' water. It is noticeable that some of these extend round the north of Scotland into the north-west North Sea, where, again, temperatures are lower than in the Channel. The results of the Channel Survey have still to be worked up in detail, but meanwhile a joint paper with Mr G. M. Spooner incorporating data from off the Dorset coast has been submitted for publication in the *Proceedings of the Dorset Natural History and Archaeological Society*.

Mr G. R. Forster has completed his notes on the underwater studies on *Echinus esculentus*, which were published in Vol. 38, No. 2 of the *Journal*. A further note in Vol. 38, No. 3 of the *Journal* has resulted from a re-examination of length measurements made on the common prawn in the light of Dr H. A. Cole's recent study of the species in North Wales. The length reached by the young prawns after 3 months' growth varies considerably from year to year and can be correlated with variations in sea temperature. A further sample of prawns was collected during the spring tides in September but has not yet been worked up.

Mr Forster has also assisted Dr G. Y. Kennedy of the Cancer Research Unit, Sheffield University, in experiments with various chemical effects on the regeneration of the sponge *Microciona atrasanguinea*. A small closed-circuit circulation is being set up in which most of the micro-organisms in the water will be killed by ultra-violet irradiation. It is hoped, in this way, to provide a certain amount of nutriment for the developing sponges and at the same time, prevent the cultures from being overgrown by Protozoa.

Aqualung diving work has been continued during the summer. Various delicate specimens were collected for the new aquarium tanks. The light cages used for feeding experiments with *Echinus* were recovered intact, though considerably distorted after 8 months on the sea floor at a depth of 9 fathoms. A few more spotted gobies have been collected. These gobies can best be coaxed out of their rocky retreats by using a garden syringe to project a jet of chlorine solution ('Domestos') into the rock crevices. The gobies are forced out of hiding, making it much easier to capture them. The method has long been used on coral reefs.

Survey work on the sessile rock fauna has been held up by the delay in delivery of some equipment, but an interesting area near the coastguard station on Hilsea Point has been examined. In this area there are a number of deep narrow gullies in the rock from which algal growth is largely excluded. Several particularly fine specimens of the sponge *Stelletta grubei* were observed; from rock scrapings Dr Eve Southward identified many small serpulids of the unusual species *Josephella maranzelleri*. This area should be well worth a more detailed survey.

Mr Q. Bone has worked upon the histology of the Acrania, and has completed two papers upon aspects of the nervous system. A study of the central nervous system in larval acraniates (*Quart. J. micr. Sci.*, Vol. 100, p. 509) has provided the first opportunity for comparison of the central nervous system of the larva with that known for the larvae of craniates, and allows some inferences as to the ancestral condition of the chordate nervous system. A detailed study of the peripheral atrial nervous system of adult amphioxus has shown that the system is predominantly sensory (it contains several rather different categories of peripheral sensory neurones), and that it is unlike the autonomic nervous systems of craniates, with which it has previously been homologized. The central nervous system of the adult amphioxus is being studied at present; preliminary results indicate that several of the components of the system have been misinterpreted, whilst others have not been noticed; it is hoped to provide a functional analysis of the components of the system which will allow comparison with the spinal cord of craniates.

In collaboration with Mr J. H. Wickstead, a paper has been published in *Nature* upon the ecology of the various types of acraniate larvae collected by Mr Wickstead from the Indo-Malayan plankton; these larvae show interesting differences in their metamorphoses which will be described at a later date.

Experiments have been carried out upon the artificial fertilization of amphioxus, and larvae successfully reared to the stage at which feeding begins; this work will be continued next season.

Physiology of Marine Organisms

Micro-anatomical investigations of light-organs often provide valuable information about the functioning of these structures. This line of approach is especially valuable when applied to deep-sea animals, in many of which the luminous response has not been observed. Dr J. A. C. Nicol has re-examined the light-organs of the piddock, *Pholas dactylus*, one of the first animals in which the luciferin-lucerase reaction was demonstrated. The light-organs contain three kinds of glandular cells: one mucus, two photogenic. It is in the latter that the luminous substrate and enzyme are elaborated. His results have been published in Vol. 39, No. 1 of the *Journal*. Dr Nicol is now examining some pelagic animals secured on cruises of R.V. 'Sarsia' and R.R.S. 'Discovery II', especially *Gnathophausia* and stomiatoid fishes. The former discharges a blue luminous secretion. The stomiatoids have conspicuous suborbital light-organs of a common pattern. These contain photocytes, the animal generating its own light, and they are provided with a mechanism for occlusion by rotating the light-emitting surface downwards. Amplifying earlier work on light emission and vision, Dr Nicol has tested the attractiveness to various animals of weak lights resembling luminescence. Some inshore crustaceans are attracted by such lights. In a simple multiple choice apparatus, the minimal intensity for attracting *Praunus neglectus* was $3 \times 10^{5}\ \mu\text{W}$ falling on 1 cm^2 at the level of the animals' eyes. The results of this work are being published in Vol. 38, No. 3 of the *Journal*. A survey of recent work on luminescence has been prepared by Dr Nicol for publication in *Biological Reviews*, Vol. 35.

Dr Nicol has also investigated the course of digestion in sea anemones, especially *Calliactis parasitica*. The process of digestion in these animals turns out to be very similar to that in *Physalia* and corals. Mesenteric filaments closely adhere to the food mass, and digest it by secreting proteases over it. Various proteins and protein degradation-products were found to stimulate digestive secretion, and the time-course of digestion of a standard meal was followed. An account of this work has been published in Vol. 38, No. 3 of the *Journal*.

The results of the joint research done by Dr Nicol and Dr G. Y. Kennedy on the pigments of *Chaetopterus* have now been published in the *Proceedings of the Royal Society*, B. The green pigment, first named 'chaetopterin' over 60 years ago by Ray Lankester, has finally been shown to be a mixture of phaeophorbides *a* and *b*. These pigments are probably derived from the breakdown of chlorophyll present in the food of the worm.

Dr E. J. Denton, in collaboration with Dr J. Gilpin-Brown, is studying the buoyancy of the cuttlefish *Sepia officinalis*. They have shown that the lamellae of the cuttlebone form independent chambers within any one of which the gases and liquid which it contains can move. When a freshly dissected cuttlebone is placed under reduced pressure liquid can readily be extracted through the posterior margins of the lamellae. The yellowish membrane which is closely applied to the bone in this region has been shown not only to have a copious blood supply, but to contain numerous ampullae close to the bone which are connected by small ducts to the veins. Cuttlefish exhibit a wide range of cuttlebone densities 0·48–0·71 and differ not in weight of dry matter but in amount of liquid which they contain. Thus a cuttlebone of density 0·7 contains about 30% (by volume) liquid, whereas a cuttlebone of density 0·5 contains about 10% liquid. The remainder of the cuttlebone contains gas, but this gas is always at less than atmospheric pressure. Cuttlefish vary in density and this variation is given entirely by changes in the density of the cuttlebone. When the cuttlebone changes in density the *mass* of gas per unit volume remains almost constant whatever the density of the cuttlebone. In a bone of reduced density the pressure of gas is therefore even lower than usual. The gas within the cuttlebone plays a completely passive role in the density changes and the pressure of gas in the cuttlebone is in no way balanced against the external hydrostatic pressure as in the swimbladder of a fish. The cuttlebone is not, however, an impermeable structure and there must be a mechanism capable of pumping salts out of the bone. The liquid inside the cuttlebone is principally a solution of sodium chloride and hypotonic to the blood and sea water, simple osmotic forces playing a major role in holding water out of the cuttlebone. The cuttlebone is very strong and only implodes at depths appreciably greater than those at which *Sepia* lives. A short note describing this work has been published in *Nature* and demonstrations 'On three ways of achieving buoyancy equilibrium in marine animals' were given at the Royal Society Conversaziones in May and June by Dr Denton, Dr Shaw and Dr Gilpin-Brown, together with Mr N. B. Marshall of the British Museum (Nat. Hist.).

Mr J. V. Howarth is collaborating with Dr Denton and Dr Gilpin-Brown in studies of the pumping mechanism of the cuttlebone.

Dr Denton found that the purple colour characteristic of the retina of freshwater fish is present in the salmon parr and smolt in fresh water, in smolt caught in the estuary and kept in sea water for several months and in estuarine salmon just returning from the sea. The two latter animals he obtained through the kindness of Dr P. F. Elson of the St Andrews Biological Station of New Brunswick. There is therefore no metamorphosis of pigments similar to that which Dr Carlisle and Dr Denton found in the freshwater eel on its return to the sea. This suggests that the salmon remains in the surface waters during its life in the ocean.

Investigations begun 2 years ago by Dr D. B. Carlisle in collaboration with Dr P. Carlson of Munich, into the comparative endocrinology of Crustacea and insects, have been widened in scope and now involve the active co-operation of Dr Peggy Ellis of the Anti-locust Research Centre, London. So far the only publication resulting from this work has been a brief communication on the ventral glands of locusts in *C.R. Acad. Sci., Paris*, T. 249, pp. 1059–60. Dr Carlisle is now devoting the major part of his attention to problems of comparative endocrinology, and with the aid of a gift of purified sheep follicle stimulating hormone donated by the United States Department of Health, Education and Welfare, he is endeavouring to determine whether this vertebrate hormone has any effect on crustacean sexual development.

He has continued his investigations into the endocrine basis of sex reversal in *Pandalus* and has begun a study of this phenomenon in the blind, burrowing reptantian *Calocaris*. An account of the anatomy and histology of those endocrine organs which are now known to be implicated in this phenomenon in *Pandalus* has appeared in Vol. 38, No. 2 of the *Journal*. Two further papers on endocrinological aspects have been published in Vol. 38, No. 3. These describe experiments and observations on the events associated with the termination of the male phase of the life history and with the beginning of the female phase, respectively. The former event is shown to be controlled mainly by the vas deferens gland and the latter by the endocrine complex of the eyestalk. *Calocaris* appears to differ from *Pandalus* in that although the testis and ovary develop successively, sperm is stored in the vas deferens till far into the female phase and probably throughout life, while the male copulatory appendages are also retained. It seems probable that although from the developmental aspect *Calocaris* is protandric, functionally it may well be a simultaneous hermaphrodite. It has no abrupt sex reversal.

The publication in Vol. 38, No. 2 of the *Journal* of Dr Carlisle's observations of the differences in the endocrinology of moulting in different populations of *Palaemon* goes far to explain the contradictory results obtained by previous workers when using different populations. The rate of moulting depends upon a fine balance between the moult-accelerating and moult-inhibiting hormones. This state of balance differs in different populations, so that the normal rate of moulting varies from one population to another, while the effect of extirpating the endocrine complex of the eyestalks may lead to either an increase or a decrease in the moult rate according to population.

Dr Carlisle has continued to work upon the Gephyrean *Priapulus* and is endeavouring to study the histology of neurosecretion in this form. His account of the neurosecretory system in another Gephyrean, *Sipunculus*, has been published in the *Gunma J. med. Sci.* in a memorial volume dedicated to the memory of the late Prof. Enami of Gunma University, Japan, with whom Dr Carlisle worked for a brief period in 1953. The neurosecretory system of *Sipunculus* shows a striking resemblance to the primitive condition of the hypothalamo-hypophysial system of vertebrates, the eyestalk complex of endocrine organs of crustaceans and the brain corpus cardium complex of insects.

Dr Carlisle has continued to employ diving equipment to study the biology of crustaceans and ascidians in their natural habitat.

In collaboration with Miss Andrée Leon and Dr R. D. Bulbrook of the Imperial Cancer Research Fund Laboratories (Royal College of Surgeons), Dr E. D. S. Corner has been studying the distribution of aryl sulphatase, β-glucuronidase and 'steroid sulphatase' among various marine invertebrates. Of the nine phyla so far examined only certain gastropod molluscs, subclass Prosobranchia, have been found to possess a 'steroid sulphatase'. Two species, *Buccinum undatum* and *Nassarius reticulatus* provide an enzyme of specificity similar to that of the 'steroid sulphatase' prepared from the land snail, *Helix pomatia*, in that it assists the hydrolysis of both aetiocholanolone and dehydro*epi*androsterone sulphates. However, the enzyme prepared from three other species, *Patella vulgata*, *Patina pellucida* and *Littorina littorea*, has a higher specificity, assisting the hydrolysis of only the latter substrate. No 'steroid sulphatase' has yet been found which will affect the hydrolysis of androsterone sulphate, but the enzyme obtained from *Nassarius* has a very high activity and should be of use in steroid analysis. Further experiments with molluscs have shown that the β-glucuronidase and aryl sulphatase activities of herbivores are, in general, greater than those of carnivores. Moreover, additional experiments using members of all the phyla examined have shown that, compared with herbivorous and carnivorous species, animals that feed on detritus are more often lacking in β-glucuronidase activity. By contrast, no correlation has been found between diet and 'steroid sulphatase' activity; and the results of studies of the behaviour of this enzyme under different experimental conditions indicate that it does not perform any physiological function related to the hydrolysis of steroid sulphates in the few species in which it has been found. An account dealing with the biochemical aspects of this work has been accepted for publication in the *Biochemical Journal*; and a second paper, concerned with the ecological aspects, has been published in Vol. 39, No. 1 of the *Journal*.

Dr Corner has continued his collaboration with Dr A. D. Boney of Plymouth Technical College in which heavy metal poisons have been used in studies of the ecological resistance of certain marine red algae. An account of this work has already appeared in Vol. 38, No. 2 of the *Journal* and the investigation is now being extended to include experiments with various fluorescent dyes and carcinogens, several of which have been found to stimulate the growth of red algae sporelings.

Dr T. I. Shaw has submitted for publication in the *Proceedings of the Royal Society* an account of his experiments relating oxygen consumption and iodine uptake by the sea weed *Laminaria digitata*. Further studies upon ^{131}I uptake by the weed have been directed towards the discovery of inhibitors which interfere with iodine uptake other than by preventing the formation of elementary iodine. Perchlorate appears to be such an inhibitor. At concentrations of a few millimolar perchlorate does not prevent the ready conversion of iodide to iodine outside the plant although it blocks the uptake of ^{131}I by freshly collected weed. However, radio-iodine uptake by plants stored overnight in the laboratory is but little affected by perchlorate. Attempts made to demonstrate that perchlorate acts by interfering with the reduction of elementary iodine in the tissues have, so far, been inconclusive.

In conjunction with Prof. A. L. Hodgkin, F.R.S., and Dr R. D. Keynes, F.R.S., both of Cambridge, and Dr P. C. Caldwell, Alan Johnston, Lawrence and Mosely Research Fellow of the Royal Society, Dr Shaw has been further investigating the effects of injection of various phosphate esters upon the active transport of sodium and potassium across the membrane of the giant nerve fibres of *Loligo*. In particular it has been shown that the injection of relatively large amounts of arginine phosphate into a nerve fibre heavily poisoned with cyanide in large measure restores to its unpoisoned level the outward movement of sodium. Moreover, the efflux is dependent upon the presence of external potassium, a characteristic feature of the efflux from unpoisoned axons. A preliminary report of these findings has been published in the *Journal of Physiology*. Currently the fate of those phosphate esters shown to affect sodium transport when injected into poisoned axons is being studied. After injection of the phosphate into a poisoned fibre the axoplasm is extruded and the water soluble components separated by chromatography. While quantitative results are not yet available, it seems clear that injection of arginine phosphate causes rapid disappearance of a compound resembling adenosine monophosphate and rapid regeneration of a compound having many of the properties of adenosine triphosphate.

Mr J. V. Howarth joined the staff as a physiologist in April. He has made an apparatus based on the Hill-Baldes thermoelectric method for the measurement of the osmotic activity of very small samples of liquid.

He has also constructed an apparatus for measuring the metabolic rate of thin strips of tissue by observing their rate of heat production. At the time of writing this apparatus has only recently been completed. A few measurements have been made on the heat production of the anterior byssus retractor muscle of *Mytilus edulis*. The preliminary results indicate that it will be possible to record the heat production of this muscle in the interesting 'fused' state which follows chemical stimulation and in which the muscle can resist great tension with apparently a minimum expenditure of energy.

Dr G. W. Bryan has been studying the uptake of radioactive caesium by marine invertebrates with a view to finding to what extent the accumulation of this ion is dependent on potassium balance. Among the decapod crustacea *Galathea squamifera*, *Carcinus maenas*, *Cancer pagurus* and *Palaemon serratus* have been used. Most of the experiments were carried out using ^{134}Cs, but in the prawn *Palaemon serratus* comparative experiments with the fission product ^{137}Cs were performed during a 2-week visit to the Windscale Works of the United Kingdom Atomic Energy Authority at the kind invitation of Mr W. L. Templeton. Rates of uptake of radioactive Cs from sea water by whole animals, their blood and principal tissues have been determined and the radioactive levels reached at equilibrium have been related to K concentration.

At 20° C equilibrium with radioactive sea water is substantially reached by *Galathea* after 200 hr. when the activity of the animal is about seven times that of an equal weight of sea water. Only 15 min. is required for the activity of the blood to reach 50 % of the equilibrium level. Uptake in the other species is a slower process. The rate of uptake of ^{134}Cs by the muscles and digestive gland of *Galathea* at 20° C is more than double the rate at 8° C. At equilibrium the blood sea-water ratio for ^{134}Cs is about the same as that for K in *Galathea*, *Carcinus* and *Cancer*. In *Palaemon* the ratio is less than unity for K and greater for Cs, while the urine blood ratio is also less than unity for K and greater for Cs. In other respects all four species are rather similar. The muscle/blood Cs ratios at equilibrium are about the same as those for K, but Cs ratios for digestive gland and the gills usually markedly exceed those for K. This is particularly noticeable in *Galathea* where the digestive gland blood Cs ratio is up to six times that for K. Reasons for this are being investigated at the present time. The effect of reduced sea-water K concentrations on the accumulation of Cs is also being studied in these animals.

Members of other phyla which have been used are the anemone *Tealia felina*, the polychaete *Perinereis cultrifera* and the nudibranch *Archidoris pseudoargus*. The whole animal sea-water ratio for Cs at equilibrium exceeds that for K in *Tealia*. A similar result is found in *Archidoris* where the tissue/blood Cs ratio exceeds that for K in all tissues except the reproductive system. In *Perinereis* the distribution of ^{134}Cs at equilibrium is almost exactly governed by tissue sea-water K ratios. Further species are being examined with a view to finding an animal which might concentrate Cs to such an extent as to be useful as an indicator of contamination of sea water with ^{137}Cs.

Dr G. T. Boalch, International Paints Research Fellow, has been investigating the toxicity of copper to the common fouling weed *Ectocarpus*. For this work a culture tank in which over 200 cultures can be grown at constant temperature and continuous illumination has been constructed. The growth of bacteria-free cultures of *Ectocarpus confervoides* treated with copper salts at varying concentrations has been investigated with this apparatus. The results so far indicate that this weed is most sensitive to copper poisoning at the early stages of growth and that as growth proceeds the extracellular products released into the culture medium give some protection against the copper.

Cultures started from 'brown felt weed' collected from the test plates of the International Paints Research Laboratory, Newton Ferrers, have shown this growth to be a stunted form of *Ectocarpus*, and laboratory cultures in which *Ectocarpus* was grown in media containing high, but not lethal, levels of copper sulphate have produced similar growth forms.

Attempts have also been made to obtain pure cultures of green and red fouling weeds, but although a green alga has been obtained in a bacteria-free condition a suitable culture medium has not yet been devised.

Library

During the year the collections of reprints and books belonging to the late Sir Sidney Harmer and to the late Dr G. P. Bidder have been arranged, catalogued and incorporated in the general index. Thanks are due to Dr Anna M. Bidder and Mrs Barclay Russell for their generosity in paying for the binding of the latter collection.

The thanks of the Association are once more due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association.

Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

Published Memoirs

Vol. 38, No. 2, of the *Journal* was published in June, and Vol. 38, No. 3 in December 1959.

The following papers, the outcome of work done at the Plymouth laboratory, have been published elsewhere than in the *Journal* of the Association:

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Armstrong, F. A. J. & Boalch, G. T., 1960. Volatile organic matter in algal culture media and sea water. *Nature, Lond.*, Vol. 185, pp. 761–2.

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Sembrat, K., 1959. Accumulation of radioactive iodine by the methylthiouracil-treated newts. True stimulation of the thyroid with the goitrogen. *Zool. Polon.*, Vol. 9, pp. 141–52.

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MEMBERSHIP OF THE ASSOCIATION

The total number of members on 31 March 1960 was 1096, being 61 more than on 31 March 1959; of these the number of life members was 125 and of annual members 971. The number of associate members is five.

GRANT FOR AQUARIUM RECONSTRUCTION

The Council wish to record their grateful thanks for the following donation towards the cost of reconstructing the Aquarium:

Shell International Petroleum Co. Ltd. £105.

DONATIONS

The Council wish to record their appreciation for the following donations to the Plymouth laboratory: Water colour paintings made by Dr E. A. Wilson on the 1910–13 British Antarctic ('Terra Nova') Expedition which had belonged to the late Mrs E. W. Sexton, and have been presented by her son, Col. F. B. W. Sexton; a cathetometer for use in the Plymouth laboratory presented by Dr J. H. Oliver.

FINANCE

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledge the following generous grants received during the year:

Fishmongers' Company (£400), The Royal Society (£100), British Association (£50), Physiological Society (£50), The Cornwall Sea Fisheries Committee (£10), The Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s*.), Leeds (£25), Durham (£10. 10*s*.), Manchester (£10. 10*s*.), Sheffield (£10. 10*s*.), Southampton (£15. 15*s*.), Reading (£10. 10*s*.), Nottingham (£10. 10*s*.), Hull (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), The Imperial College of Science and Technology (£10), Gonville and Caius College, Cambridge (£5), and The Zoological Society of London (£10. 10*s*.).

PRESIDENT, VICE-PRESIDENTS, OFFICERS AND COUNCIL:

The following is the list of those proposed by the Council for election for the year 1960–61:

President

Prof. C. F. A. PANTIN, Sc.D., F.R.S.

Vice-Presidents

THE EARL OF IVEAGH, K.G., C.B., C.M.G.
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., LL.D., F.R.S.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., F.R.S.
A. T. A. DOBSON, C.B., C.V.O., C.B.E.
Major E. G. CHRISTIE-MILLER
MORLEY H. NEALE, C.B.E.
THE EARL OF VERULAM
Prof. Sir JAMES GRAY, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S.
G. M. GRAHAM, C.M.G., O.B.E.

COUNCIL

To retire in 1961

H. A. COLE, D.Sc.
Prof. J. E. HARRIS, Ph.D., F.R.S.
Prof. C. M. YONGE, C.B.E., D.Sc., F.R.S.
G. E. FOGG, Ph.D.
C. E. LUCAS, C.M.G., D.Sc.

To retire in 1962

J. N. CARRUTHERS, D.Sc., F.Inst.P.
Prof. A. L. HODGKIN, F.R.S.
Prof. O. E. LOWENSTEIN, D.Sc., F.R.S.
Prof. G. E. NEWELL, T.D., D.Sc.
Prof. W. F. WHITTARD, D.Sc., F.R.S.

To retire in 1963

G. E. R. DEACON, C.B.E., D.Sc., F.R.S.
F. C. FRASER, D.Sc.
M. N. HILL, Ph.D.
O. D. HUNT, F.R.S.E.
Prof. G. P. WELLS, Sc.D., F.R.S.

Hon. Treasurer

HARRISON S. EDWARDS, Westhumble Lacey, near Dorking, Surrey

Secretary

F. S. RUSSELL, C.B.E., D.S.C., D.F.C., LL.D., F.R.S.
The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

B. C. ENGHOLM (Ministry of Agriculture, Fisheries and Food)
The Worshipful Company of Fishmongers:
  The Prime Warden
  Major E. G. CHRISTIE-MILLER
  HARRISON S. EDWARDS
Prof. Sir ALISTER HARDY, Kt., D.Sc., F.R.S. (Oxford University)
Prof. C. F. A. PANTIN, Sc.D., F.R.S. (Cambridge University)
EDWARD HINDLE, Sc.D., F.R.S. (British Association)
N. B. MARSHALL (Zoological Society)
Prof. Sir JAMES GRAY, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S. (Royal Society)

BALANCE SHEET 1959–60

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31 MARCH 1960

		£	£
CAPITAL RESERVE ACCOUNT:			
As at 31 March 1959		171,005	
Add: Expenditure on fixed assets recovered		490	
		171,495	
Less: Transfer to surplus account being an amount equivalent to the depreciation provided on assets acquired out of Development Fund grants		3,674	
			167,821
SURPLUS ACCOUNT:			
As at 31 March 1959		9,478	
Add: Transfer from Capital Reserve Account		3,674	
		13,152	
Deduct:			
Increase in provision for diminution in value of General Fund investments	65		
Excess of expenditure over income for the year	826		
		891	
			12,261
			180,082
BALANCES ON SPECIAL FUNDS (see annexed statement)			5,365
CURRENT LIABILITIES:			
Sundry creditors and accrued expenses		3,468	
Subscriptions and grants received in advance		327	
			3,795
			£189,242

Note: Capital commitments outstanding amount to approximately £2,730 (1959 £8,695) of which £1,500 (1959 £7,550) is recoverable

O. E. LOWENSTEIN
W. F. WHITTARD } *Members of the Council*

	£ Cost or Valuation	£ Depreciation	£
FIXED ASSETS:			
Boats and equipment:			
At cost:			
R.V. 'Sarsia'	137,761	9,808	127,953
M.F.V. 'Sula'	12,500	1,210	11,290
R.L. 'Gammarus'	200	30	170
	150,461	11,048	139,413
Laboratory apparatus, equipment and machinery: At cost	17,669	6,554	11,115
Library at valuation in 1941 plus additions as valued by the Director	24,440	—	24,440
	£192,570	£17,602	
			174,968
INVESTMENTS AT MARKET VALUE:			
General Fund (including Composition Fees) at book amount (Market value £1,368; last year £1,370)		1,814	
E. T. Browne Bequest Funds at cost (Market value £3,400; last year £3,431)		4,817	
		6,631	
Less: Provision for diminution in value of investments		1,863	
			4,768
CURRENT ASSETS:			
Stocks on hand as valued by the Director		4,515	
Sundry debtors and prepayments		2,112	
Balances at bankers and cash in hand		2,879	
			9,506
			£189,242

AUDITORS' REPORT TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31 March 1960 and of its excess of expenditure over income for the year ended on that date.

We have obtained all the information and explanations which we considered necessary. In our opinion the Association has kept proper books and the said accounts which are in agreement with them and with the said information and explanations, give in the prescribed manner the information required by the Companies Act 1948.

Norwich Union House
2 St Andrew's Cross
Plymouth
12 *May* 1960

PRICE WATERHOUSE & CO.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31 MARCH 1960

	£	£
Salaries (including additional for previous year) National Insurance, Superannuation Scheme Contributions and Supplementary Pensions		42,028
Laboratory's and Boats' Crews' Wages (including additional for previous years), National Insurance, Superannuation Scheme Contributions, Pensions and Employers' Liability Insurance		37,784
Upkeep of Library		980
Scientific Publications, *less* Sales		1,985
Upkeep of Laboratories:		
Buildings and machinery	1,145	
Electricity, gas, coal and water	1,470	
Chemicals and apparatus	3,188	
Depreciation of laboratory apparatus, equipment and machinery	1,234	
Rents and insurance	437	
Travelling expenses	1,237	
Audit fee	175	
Stationery, postage, telephone and sundries	1,585	
Specimens	139	
Collecting expenses and upkeep of truck	237	
		10,847
Maintenance and Operation of Boats:		
Petrol, oil, paraffin, etc.	1,782	
Maintenance and repairs	7,364	
Depreciation	3,674	
Insurances	2,303	
Hire of Decca Navigator—R.V. 'Sarsia'	395	
		15,518
Entertainment Expenses		79
Bank Charges, *less* Interest on Bank Deposits		15
		£109,236

	£	£	£
Grants and Table Rents:			
Ministry of Agriculture, Fisheries and Food—Grant from Development Fund		99,477	
Fishmongers' Company		400	
Miscellaneous (including Royal Society £100, British Association £50, Physiological Society £50, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s*., Leeds £25, Southampton £15. 15*s*., Durham £10. 10*s*., Exeter £10. 10*s*., Leicester £10. 10*s*., Manchester £10. 10*s*., Nottingham £10*s*. 10*s*., Hull £10. 10*s*., Reading £10. 10*s*., and Sheffield £10. 10*s*., Imperial College £10, Zoological Society of London £10. 10*s*., Ministry of Works £112, Imperial Chemical Industries Ltd., £52. 10*s*., International Paints Ltd. £52. 10*s*., Gonville and Caius College, Cambridge £5)		1,481	
			101,358
Subscriptions			1,092
Sales:			
Specimens		3,306	
Fish		341	
	£		
Nets, gear and hydrographical equipment	916		
Less: Cost of materials	709		
		207	
			3,854
Income from Investments			62
Aquarium:			
Admission fees		2,425	
Sale of guides		38	
		2,463	
Less: Maintenance, printing and advertising		419	
			2,044
Balance being excess of expenditure over income for the year			826
			£109,236

MOVEMENTS ON SPECIAL FUNDS DURING THE YEAR TO 31 MARCH 1960

	E. T. Browne Bequest									
	Library £	Special Apparatus £	Scientific Publications £	Aquarium Reconstruction Fund £	Rockefeller Foundation Fund £	Library Extension and Dogfish House Fund £	Reservoir and Sea Water Tanks Fund £	Library Reserve Fund £	Research Funds* £	TOTAL £
BALANCES AT 31 MARCH 1959 (after providing £1,258 for diminution in value of investments)	1,058	2,070	656	1,141	501	697	(905)	—	243	5,461
Add: Income during year										
Grants (including amounts paid direct to the contractors by the Nuffield Foundation)	—	—	—	7,075	—	—	—	—	4,376	11,451
Income from investments	41	84	30	—	—	—	—	—	—	155
Bank deposit interest	—	—	—	26	—	15	—	—	—	41
Other income	—	—	102	—	—	—	—	325	—	427
Transfer from Library Extension and Dogfish House Fund	—	—	—	—	—	—	712	—	—	712
	1,099	2,154	788	8,242	501	712	(193)	325	4,619	18,247
Deduct: Expenditure during year	—	134	—	7,002	501	—	—	93	4,281	12,011
Increase in provision for diminution in value of investments	40	84	35	—	—	—	—	—	—	159
Transfer to Reservoir and Sea Water Tanks Fund	—	—	—	—	—	712	—	—	—	712
BALANCES AT 31 MARCH 1960	£1,059	£1,936	£753	£1,240	—	—	£(193)	£232	£338	£5,365

* Including International Paints Limited Research Fellowship.

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LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1960

GOVERNORS

The British Association for the Advancement of Science, 18 Adam Street, London, W.C. 2
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 48 Fenchurch Street, London, E.C. 3
The Worshipful Company of Fishmongers, Fishmongers Hall, London, E.C. 4
  The Prime Warden. (**Council**, 1886→)
  Edwards, Harrison S., Westhumble Lacey, near Dorking, Surrey. (**Council**, 1950→; **Hon. Treasurer**, 1956→)
  Christie-Miller, Major E. G., 38 Hyde Park Street, London, W. 2. (**Council**, 1941→; **Hon. Treasurer**, 1941→56; **Vice-President**, 1951→)
The Zoological Society of London, Regent's Park, London, N.W. 1
The Royal Society, Burlington House, Piccadilly, London, W. 1
Ministry of Agriculture, Fisheries & Food, 3 Whitehall Place, London, S.W. 1
Bayly, Robert (the late). (**Council**, 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council**, 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council**, 1896–1903)
Bidder, G. P., Sc.D. (the late). (**Council**, 1899–1953; **President**, 1939–45; **Vice-President**, 1948–53)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President**, 1929; 1939–45; **President**, 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary). (**Council**, 1895–1942; **Secretary**, 1895–1936; **Hon. Governor**, 1937–42)

FOUNDERS

1884 The Corporation of the City of London, The Guildhall, London, E.C. 3
1884 The Worshipful Company of Mercers, Mercers' Hall, 4 Ironmonger Lane London, E.C. 2
1884 The Worshipful Company of Goldsmiths, Goldsmiths' Hall, Foster Lane, London, E.C. 2
1884 The Royal Microscopical Society, B.M.A. House, Tavistock Square, London, W.C. 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council**, 1884–92; **Hon. Treasurer**, 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiot, John P. (the late)

1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary**, 1884–90; **President**, 1891–1929)
1884 Lord Masham (the late)
1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, (the late)
1888 The Worshipful Company of Drapers, Drapers' Hall, London, E.C. 2
1889 The Worshipful Company of Grocers, Grocers' Hall, Princes Street, London, E.C. 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. Hansford, M.Inst.C.E. (the late)
1899 The Earl of Iveagh, K.G., C.B., C.M.G., 11 St James's Square, London, S.W. 1 (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc. (the late). (**Council**, 1932–5)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 Phillimore Gardens, London, W. 8
1920 Lord Buckland of Bwlch (the late)
1920 Llewellyn, Sir D. R. (the late)
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., Ocean House, Pudding Lane, London, E.C. 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, Great George Street, Westminster, London, S.W. 1
1925 Discovery Committee
1927 Bidder, Miss Anna M., Ph.D., 2a Cavendish Avenue, Hills Road, Cambridge. (**Council**, 1948–51, 1954–57)
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., c/o Messrs Peel and Co., Ltd. P.O. Box 331, Alexandria, Egypt. (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W. (the late)

MEMBERS

* Life Members

1949 Abbott, B. C., Ph.D., F.Inst. P., Dept. of Zoology, University of California, Los Angeles 24, Calif., U.S.A.
1945 Aberdeen University Library, The University, Aberdeen
1957 Achurch, Mrs R., 235 Park Road, Peterborough, Northants
1934 Adam, Mrs K. M. G., 84 Lasswade Road, Edinburgh 9
1951 Adams, E., 2 Woodford Crescent, Marsh Mills, Plympton, Devon
1960 Adams, Miss I. M., The Laboratory, Citadel Hill, Plymouth, Devon
1960 Adams, J. A., Egypt, New Aberdour, Fraserborough, Aberdeens
*1954 Adams, Miss M. N. E., 11 Milner Road, Kingston-on-Thames, Surrey
1957 Adcock, N. W., Rossignol, Harlaxton Drive, Long Eaton, Notts
1940 Lord Adrian, O.M., M.D., D.Sc., LL.D., F.R.S., The Master's Lodge, Trinity College, Cambridge
1947 Affleck, R. J., 1 Helmsdale Road, London, S.W. 16
1957 Agrawal, V. P., D.A.V. College, Muzaffarnagar (V.P.). India
1957 Akkeshi Marine Biological Station, Akkeshi, Hokkaido, Japan
1959 Alexander, J. E. A., The Marine Laboratory, University of Miami, Rickenbacker Causeway, Virginia Key, Miami 49, Fla., U.S.A.
1950 Alexandrowicz, J. S., Ph.D., M.D., The Laboratory, Citadel Hill, Plymouth, Devon
1954 Allen, G. L., The Nook, 87A Bury Old Road, Sedgley Park, Prestwich, Manchester
1951 Allen, J. A., Dove Marine Laboratory, Cullercoats, Northumbs
1952 Allen, Miss J. M., Tenements Farm, Chipperfield, Herts
1953 Alvariño, Señora A., P.O. Box 109, La Jolla, Calif., U.S.A.
*1927 Amirthalingam, C., Ph.D., University of Ceylon, Peradeniya, Ceylon
1957 Angus, L. H., A.R.I.C., Three Gables, Torridge, Plympton, Plymouth, Devon
1956 Ansell, A. D., Dept. of Zoology, The University, Glasgow, W. 2
1958 Arai, Mrs Mary Needler, Dept. of Zoology, University of British Columbia, Vancouver 8, B.C., Canada
1959 Arakawa, R., 120 East Grand Street, Berea, Ohio, U.S.A.
1950 Arnold, D. C., Bede College, Durham
1944 Ashby, D. G., c/o P.O. Box 61, Stellenbosch, Cape Province, S. Africa
1954 Ashhurst, Miss D. E., Dept. of Entomology and Economic Zoology, Institute of Agriculture, University of Minnesota, St Paul 1, Minn., U.S.A.
1958 Atherton, D., Ph.D., J. S. Craig & Co. Ltd., 87 Portman Street, Glasgow, S. 1
*1929 Atkins, Miss D., D.Sc., c/o The Laboratory, Citadel Hill, Plymouth, Devon
*1910 Atkinson, G. T., Gresham House, Esplanade, Lowestoft, Suffolk
1959 Atkinson, Miss Kathleen M., Marine Station, Millport, Isle of Cumbrae, Scotland
1951 Atlantic Biological Station, St Andrews, N.B., Canada

1948 Baal, H. J., 3 Bel Royal Villas, Jersey, C.I.
1957 Baer, Prof. J. G., Institut de Zoologie, Rue Emile Argand, Neuchâtel, Switzerland
1950 Baerends, Prof. G. P., Zoölogisch Laboratorium, Rijksstraatweg 78, Haren (Gron.), Holland
*1949 Bagenal, T. B., Marine Station, Millport, Isle of Cumbrae, Scotland

1956 Bailey, Miss J. A., 20 Christchurch Gardens, Epsom, Surrey
*1952 Baily, Joshua L., Jr., 4435 Ampudia Street, San Diego 3, Calif., U.S.A.
1950 Bainbridge, R., Ph.D., 43 Strathmore Avenue, Hull
1953 Bainbridge, V., Oceanographic Laboratory, 78 Craighall Road, Edinburgh 6
1957 Baker, C. J. E., Dept. of Biology, University College of North Staffordshire, Keele, Staffs.
*1920 Baker, J. R., D.Sc., F.R.S., Dept. of Zoology and Comparative Anatomy, University Museum, Oxford
1936 Baldwin, Prof. E., Ph.D., Department of Biochemistry, University College, Gower Street, London, W.C. 1. (**Council**, 1946–48, 1957–60)
1955 Ballantine, W. J., Zoology Dept., Queen Mary College, Mile End Road, London, E. 1
1959 Balls, M., 19 Hill Street, Norwich, Norfolk
1959 Bande, V. N. Central Marine Fisheries Research Sub-station, Botawalla Chambers, Sir P. M. Road, Bombay 1, India
1955 Banks, Mrs P. B. J., Upper Flat, 11, Crossways, Shenfield, Sussex
1953 Barker, J. A., 8 Hillside Avenue, Friern Barnet, London, N. 11
1949 Barnard, Surg.-Lt., E. E. P., R.N., 16 Kings Road, Southsea, Hants
1956 Barnard, J. Laurens, Ph.D., Allan Hancock Foundation, University of California, Los Angeles 7, Calif., U.S.A.
1939 Barnes, H., D.Sc., F.R.I.C., Marine Station, Millport, Isle of Cumbrae, Scotland
1954 Barnes, M. McC., Mandeville, Rosebank Crescent, Pennsylvania, Exeter, Devon
1955 Barnett, P. R. O., Ph.D., Marine Station, Millport, Isle of Cumbrae, Scotland
1953 Barns, H. N., Devonia, Sidmouth Street, Seaton, Devon
1957 Barr, W. A., 238a Main Street, Bellshill, Lanarks
1939 Barrington, Prof. E. J. W., D.Sc., Dept. of Zoology, The University, Nottingham
1951 Barron, H., 65 Sumerton Road, Belfast, N. Ireland
1939 Bassindale, R., Dept. of Zoology, The University, Bristol 8
*1946 Batham, Miss E. J., Ph.D., Portobello Marine Biological Station, Portobello, Otago, New Zealand
1939 Baxter, E. W., Ph.D., Biology Dept., Medical School, Guy's Hospital, London, S.E. 1
*1929 Baylis, L. E., Ph.D., Dept. of Physiology, University College, Gower Street, London, W.C. 1
1934 Beadle, L. C., Dept. of Biology, University College of East Africa, P.O. Box 262, Kampala, Uganda
1957 Beard, D. M. MacG., 123 Northcote Road, Downend, Bristol
1928 Beer, Sir Gavin de, Kt., D.Sc., F.R.S., 39, Shrewsbury House, Cheyne Walk, London, S.W. 3
1955 Beeson, Miss G., Redgate, 216 Unthank Road, Norwich, Norfolk
1954 Belcher, J. H., Ph.D., The Ferry House, Far Sawrey, Ambleside, Westmorland
1950 Bell, Mrs E. B., 23 Teck Street, Saint John, New Brunswick, Canada
1958 Bellairs Research Institute of McGill University, St James, Barbados, B.W.I.
1957 Bennett, D. P., 15 Pickering Road, Cheltenham, Glos
1959 Berguist, Mrs P. R., c/o Zoology Dept., University of Auckland, Box 2553, Auckland, New Zealand

1960 Berkson, H., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1954 Berner, L. D., Jr., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1958 Bernhard, Dr Michael, C.N.R.N., Fiascherino, Provincia La Spezia, Italy
1947 Berrill, Prof. N. J., F.R.S., Dept. of Zoology, McGill University, Montreal, Canada
1955 Berry, R. J., Ph.D., Group for Experimental Research in Inherited Diseases, University College, Gower Street, London, W.C. 1
1947 Best, A. C. G., The Laboratory, Citadel Hill, Plymouth, Devon
1959 Beynon, Miss M., Bryndedwydd, St David's Road, Aberystwyth, Cards
1953 Bhimachar, B. S., D.Sc., F.N.I., Central Inland Fisheries Research Station, 47/1 Strand Road, Calcutta 7, India
1958 Bhupendra, P., Marine Biology Station, Menai Bridge, Anglesey
1903 Bidder, Col. H. F., The Malting House, Nettlebed, near Henley-on-Thames, Oxon
1957 Bieri, R., Ph.D., 116 Glen Street, Yellow Springs, Ohio, U.S.A.
*1945 Bingley, F. J., Flatford Mill Field Centre, East Bergholt, near Colchester, Essex
1955 Binyon, E. J., Ph.D., Royal Holloway College, Englefield Green, Surrey
1925 Birkbeck College, The Library, Malet Street, London, W.C. 1
1951 Birket, L., Fisheries Laboratory, Lowestoft, Suffolk
1947 Bishop, M. W. H., Meadow Farm, Waterbeach, Cambs
1960 Blackburn, Miss D. M., South Devon and East Cornwall Hospital, Devonport, Plymouth, Devon
1951 Blackburn, Prof. M., D.Sc., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1960 Blackler, Miss M. C. H., Ph.D., Gatty Marine Laboratory, St Andrews, Fife
1957 Blake, J. W., Dept. of Zoology, University of North Carolina, Chapel Hill, N.C., U.S.A.
1930 Blaschko, H. K. F., Ph.D., Dept. of Pharmacology, South Parks Road, Oxford
1952 Blaxter, J. H. S., Marine Laboratory, Victoria Road, Torry, Aberdeen
1957 Blood, M. J., Wingfields, Gander Hill, Haywards Heath, Sussex
1953 Boalch, G. T., Ph.D., c/o The Laboratory, Citadel Hill, Plymouth, Devon
1957 Bocks, Miss S. M., 29 Milford Street, London, S.W. 8
1951 Boden, B. P., Ph.D., Scripps Institution of Oceanography, La Jolla, Calif., U.S.A.
1947 Boëtius, Dr Jan, Fysiologisk Laboratorium, Danmarks Akvarium, Charlottenlund, Denmark
1936 Bogue, Prof. J. Yule, D.Sc., Heyscroft, Hartley Road, Altrincham, Cheshire
1932 Bolitho, Capt. R. J. B., Gorey, Jersey, C.I.
1959 Bone, Q., The Laboratory, Citadel Hill, Plymouth, Devon
1945 Boney, A. D., Ph.D., 3 Merafield Close, Plympton, Plymouth, Devon
1954 Bonham, Dr K., Applied Fisheries Laboratory, University of Washington, Seattle, Wash., U.S.A.
1957 Boolootian, R. A., Ph.D., Dept. of Zoology, University of California, Los Angeles 24, Calif., U.S.A.
1957 Booth, Miss M. A., 21 Pinfold Lane, Penn, Wolverhampton, Staffs
*1933 Boschma, Prof. Dr H., Rijksmuseum van Natuurlijke Historie, Leiden, Holland
1959 Boss, K. J., Dept. of Zoology, Michigan State University, East Lansing, Mich., U.S.A.

1947 Bossanyi, J., 22 Field End Road, Eastcote, Pinner, Middx
1959 Bowden, J., M.B., Ph.D., Dept. of Zoology, The University, Glasgow, W.2
1954 Bowers, A. B., Marine Biological Station, Port Erin, Isle of Man
1959 Boycott, B. B., Zoology Dept., University College, Gower Street, London, W.C.1
1955 Bradley, D. J., 71 Linden Drive, Evington, Leicester
*1954 Bradshaw, J. S., P.O. Box 891, Del Mar, Calif., U.S.A.
1959 Brafield, A. E., 120 Woodlands Avenue, Wanstead, London, E.11
1957 Brailsford, J. D., 328 London Road, Wokingham, Berks
1940 Brambell, Prof. F. W. Rogers, D.Sc., F.R.S., Dept. of Zoology, University College of North Wales, Bangor, Caern. (**Council** 1944–47, 1948–51)
1954 Brehaut, R. N., La Canurie, Collings Road, St Peter Port, Guernsey, C.I.
1959 Bridges, Dr C. D. B., Visual Research Division (Medical Research Council), Institute of Ophthalmology, Judd Street, London, W.C.1
1924 Brightwell, L. R., East Cliff Cottage, West Portholland, Portloe, Truro, Cornwall
1958 Brimson, P. W., The Rectory, Old Cleeve, Minehead, Som
1933 Bristol University, Dept. of Zoology, Bristol 8
*1941 British Celanese, Ltd., Celanese House, Hanover Square, London, W.1
1939 British Ropes Ltd., Western Avenue, Cardiff
1958 British Sub-Aqua Club, Taunton Branch, The Secretary, Two Lilac Cottage, Trull, Taunton, Som
1955 British Sub-Aqua Club, Scientific Section, The Close, Newport Pagnell, Bucks
*1946 Brock, Mrs C. H., Ph.D., 32 Barton Road, Cambridge
1946 Brough, Prof. James, D.Sc., Dept. of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff
1955 Brown, C. A., 26 Sydney Road, Newquay, Cornwall
1928 Brown, Miss E. M., Ph.D., 6 Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey
1936 Brown, Herbert H., O.B.E., Ph.D., Fisheries Division, F.A.O.U.N., Viale delle Terme di Caracalla, Rome, Italy
1959 Brown, M. C., 53 Southway, Totteridge, London, N.20
1955 Bruce, Dr A. J., East African Marine Fisheries Research Organisation, P.O. Box 668, Zanzibar
1958 Brunet, P. C. J., D.Phil., Dept. of Zoology, University Museum, Oxford
1953 Buchsbaum, Prof. R., Ph.D., Dept. of Biological Sciences, University of Pittsburgh, Pittsburgh 13, Penna., U.S.A.
1953 Buckee, R. E., 32 Weston Drive, Stanmore, Middx
*1925 Bull, Herbert O., D.Sc., Dove Marine Laboratory, Cullercoats, Northumbs
1955 Burch, J. Q., 4206 Halldale Avenue, Los Angeles 62, Calif., U.S.A.
1951 Burgess, G. H. O., D.S.I.R., Humber Laboratory, Wassand Street, Hull
1954 Burley, Miss E. A. M., Avondale, 2 Narborough Road South, Leicester
1948 Burrows, Mrs E. M., Ph.D., Hartley Botanical Laboratories, The University, Liverpool 3
1954 Burt, Wayne V., Ph.D., Chairman, Dept. of Oceanography, Oregon State College, Corvallis, Ore., U.S.A.
1947 Burton, R. F., Pinecroft, Ockham Road North, East Horsley, Surrey
1959 Burwell, W. R., 11 Claremont Grove, Exmouth, Devon
1949 Bush, Prof. S. F., D.Phil., Dept. of Zoology, University of Natal, Pietermaritzburgh, S. Africa

1949 Butcher, A. W., Three Salmons Hotel, Usk, Mon
1960 Butcher, R. W., Ph.D., Fisheries Laboratory, Burnham-on-Crouch, Essex

1955 Caldwell, P. C., D.Phil, Dept. of Zoology, The University, Bristol 8
1955 Caldwell, Mrs P. C., c/o Dept. of Zoology, The University, Bristol 8
1949 Cameron, H. D., Bramley Tor, 43 Seymour Park, Mannamead, Plymouth, Devon
1959 Cameron, P. F., D.Obst., R.C.O.G., c/o Bridge Cottage, Perran-ar-Worthal, near Truro, Cornwall
*1950 Cameron, Dr W. M., Defence Research Board, Ottawa, Ontario, Canada
1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., Dept. of Zoology, The University, Manchester 13. (**Council**, 1927–30, 1932–34, 1937–41, 1942–45, 1952–55)
1954 Canterbury Museum, Rolleston Avenue, Christchurch, New Zealand
1950 Capstick, C. K., Ph.D., The United Steel Companies Ltd., Dept. of Operational Research and Cybernetics, Cybor House, 1 Tapton House Road, Sheffield 10
1958 Carr, M. R., 41 Great Tattenhams, Epsom Downs, Surrey
1953 Carr-Saunders, E. M., 51 Brompton Square, London, S.W.3
1956 Carrie, B. G. A., Carisbrooke, Milverton Road, Totton, Hants
1958 Carriker, M. R., Ph.D., Dept. of Zoology, University of North Carolina, Chapel Hill, N.C., U.S.A.
1927 Carruthers, J. N., D.Sc., F.Inst.P., National Institute of Oceanography, Wormley, Godalming, Surrey. (**Council**, 1948–51, 1953–56, 1959 →)
1923 Carter, G. S., Ph.D., Dept. of Zoology, Downing Street, Cambridge
1957 Caspers, Prof. Dr H., Zoologisches Staatsinstitut, Bornplatz 5, Hamburg 13, Germany
1959 Cassie, R. M., New Zealand Oceanographic Institute, D.S.I.R., P.O. Box 8009, Wellington, New Zealand
*1931 Cattell, Dr McKeen, Cornell University Medical College, 477 First Avenue, New York City, U.S.A.
*1948 Cattley, J. G., Fisheries Laboratory, Lowestoft, Suffolk
1959 Caunter, Brig. J. A. L., C.B.E., M.C., The Brentons, Hannafore, Looe, Cornwall
1949 Centre de Recherches et d'Etudes Océanographiques, 1 Quai Branly, Paris VII, France
1958 Chadwick, N. L., 6 Paul's Dene Road, Salisbury, Wilts
1958 Chamberlain, N. A., Chesapeake Bay Institute, The Johns Hopkins University, Baltimore 18, Md., U.S.A.
*1949 Chang, H. W., Zoological Institute, Academia Sinica, 320 Yo Yang Road, Shanghai, China
1957 Changeux, Jean-Pierre, 45 rue d'VIm, Paris V^e, France
*1952 Chaplin, Viscount, Wadstray House, Blackawton, near Totnes, Devon
*1949 Chapman, Prof. Garth, Ph.D., Nunns, Coxtie Green, Brentwood, Essex
1953 Chapman, Mrs R. F., 19 Long Lodge Drive, Walton-on-Thames, Surrey
1936 Charterhouse School, Biological Dept., Godalming, Surrey
1958 Chatfield, C. I., 96 Weston Park Road, Peverell, Plymouth, Devon
1947 Cheng, Prof. Chung, Ph.D., Dept. of Oceanography, National Amoy University, Amoy, China
*1947 Chidambaram, K., Fisheries Biological Station, West Hill Post, South Malabar, India
1952 Childs, P., F.R.C.S., 8 The Crescent, Plymouth, Devon
1953 Chile: Dr Parmenio Yanez Andrade, Director, Marine Biological Station of the University of Chile, Casilla 13-D, Vina del Mar, Chile

*1958 Chin, E., 4312 Avenue 0½, Galveston, Texas, U.S.A.
1946 Chipperfield, Philip N. J., Ph.D., Hillside, Manor Road, Brixham, Devon
1958 Choi, Prof. Ki-Chul, College of Education, Seoul National University, Seoul, Korea
1942 Christie-Miller, Major E. G., 38 Hyde Park Street, London, W. 2. (**Council**, 1941 →; **Hon. Treasurer**, 1941–56; **Vice-President**, 1951 →).
1959 Chubb, J. C., Dept. of Zoology, The University, Liverpool
1952 Clark, J. T., 36 Angel Road, Harrow, Middx
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